

PRODEINOTHERIUM FROM GEBEL ZELTEN,
LIBYA



BY

JOHN MICHAEL HARRIS *ref.*

Centre for Prehistory and Palaeontology, Nairobi

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By J. M. HARRIS

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SYNOPSIS

A large assemblage of vertebrate fossils has been collected from Miocene continental and near-shore marine lithosomes at the Gebel Zelten, Libya. Deinotheres were not prolific but are of interest in that they include the most complete skull yet discovered, plus the associated skull, mandible and partial skeleton of an immature individual. These are described and compared with other deinotheres remains and with the postcranial skeleton of fossil and recent elephantoid proboscideans.

Features of the skull, skeleton and dentition indicate that the family Deinotheriidae possessed two genera and Elik's taxon *Prodeinotherium* is resurrected for the earlier and more primitive genus to which the Gebel Zelten specimens belong. The facial region of the Libyan *Prodeinotherium* skull has a downcurved rostrum that is modified to bear a proboscis. The occipital region, basicranium and anterior cervical vertebrae are adapted to impart a powerful downward thrust to the tusks. The cheek teeth are separated into an anterior crushing battery and a posterior shearing battery.

The postcranial skeleton of *Prodeinotherium* and *Deinotherium* exhibit graviportal adaptations for support of the body weight. The atlas and axis vertebrae of deinotheres are distinctive and other differences in the postcranial skeleton from that of elephantoids may be detected. The scapula and foot bones of *Prodeinotherium* may be readily recognized but the long bones resemble those of *Elephas*. More advanced characters shown by *Deinotherium* include reduction of the scapular spine, shortening of the femur, elongation of the manus and pes, and reduction of the first digit thus leading to functional tetradactyly. These may all be interpreted as cursorial adaptations.

I. ABBREVIATIONS AND ACKNOWLEDGEMENTS

Individual specimens from Gebel Zelten are referred to by their University of Bristol accession numbers, e.g. 6404 : 44, 6418 : 20 (M.26665). Specimens of *Deinotherium giganteum* from Höwenegg, Germany, and currently at the Johannes Wurtemberg Universitaat, Mainz, had not been given permanent accession numbers at the time of writing and are referred to in tables of measurements as 'Höwenegg'. Recent specimens of *Loxodonta africana* used for comparison in the section on the axial skeleton include OM 2209 from the National Museum of Kenya and 1961.8.9.82 from the British Museum (Natural History). Comparison between the appendicular skeleton of *Prodeinotherium* and *Elephas maximus* was based on the skeleton of an Indian elephant in the University of Bristol Department of Geology (catalogue number U.B.20189). Deinotherere material with KNM catalogue numbers is from the Centre for Prehistory and Palaeontology, Nairobi. The catalogue numbers of mammalian specimens from the British Museum (Natural History) are prefaced by B.M.(N.H.)M. or (in tables of measurements) M. In the tables, measurements are given in cms. unless otherwise stated; * = approximate measurement, + = incomplete specimen.

This paper formed part of a Ph.D. thesis from the University of Bristol that was supervised by Dr R. J. G. Savage for whose help and encouragement I am very grateful. The work was financed by a grant from N.E.R.C. I am grateful also to Mrs D. M. Leakey who read and criticised the manuscript.

Prodeinotherium skull M.26665 was prepared by Mr A. Rixon in the Department of Palaeontology, British Museum (Natural History). Deinotherere material from the 1964 and 1966 University of Bristol expeditions was prepared by Mr. M. White of the Department of Geology, University of Bristol. The photographs were prepared by Mr R. Godwin and line drawings of the postcranial material by Mrs M. Clapp.

Field work in Libya was made possible by generous co-operation from Esso Standard Libya and Oasis Oil Company of Libya Inc.

I am indebted to the staff of the various institutions that have permitted me to examine material in their collections, and especially the late Professor C. Arambourg (Institut de Paleontologie, Paris), Professor H. Tobelin (Johannes Wurtemberg Universitaat, Mainz), Professor R. Dehm (Institut für Paläontologie, Munich), Dr E. Aguirre (Museo de Ciencias Naturales, Madrid), Dr L. S. B. Leakey (Centre for Prehistory and Palaeontology, Nairobi), and Dr A. Sutcliffe (Department of Palaeontology, British Museum (Natural History)).

II. INTRODUCTION

THE Gebel Zelten is an elongate mesa lying approximately 200 kms inland from the Gulf of Sirte and is bounded by the co-ordinates $19\frac{1}{2}^{\circ}$ – $20\frac{1}{2}^{\circ}$ E and 28° – 29° N. The gebel extends for some 140 kms in a northwest-southwest direction. It attains a height of some 40–60 metres at its western extremity but gradually decreases in elevation towards the east until it merges with the Calenscio Serir. At the eastern extremity of the gebel the northern and southern scarps are separated by a distance of some 50 kms. The scarps converge towards the west and near the centre of the gebel they are only 8 kms apart. West of this point the southern scarp diverges

sharply from the northern before merging at the extreme western extremity (see text-fig. 1). The Gebel Zelten is deeply dissected by wadis that often reach 3 kms in length. Most of the vertebrate sites are located in branches of the wadi systems.

The rocks exposed at the Gebel Zelten are of Miocene age and were attributed by Selley (1966) to the Marada Formation. The rocks represent the mixed fluvio-marine facies of the southern part of the Sirte Basin. The succession at Gebel Zelten is predominantly of sandstone, sandy shales and shales, the units dipping northward at an angle of about six seconds (Doust, 1968). According to Doust, the base of the section at the northern scarp consists of intertidal and fluvial sands and shales that pass upward into bioturbated calcarenites and calcisilicates representing intertidal and subtidal facies. The top of the succession comprises calcareous crossbedded sandstones from an estuarine channel facies. On the southern scarp a mixed intertidal and fluvial facies passes upwards into intertidal sediments that are ultimately overlain by the estuarine channel facies. Detailed discussions of the geology are given in Selley (1966, 1967, 1968), Doust (1968), and Magnier (1962, 1968).

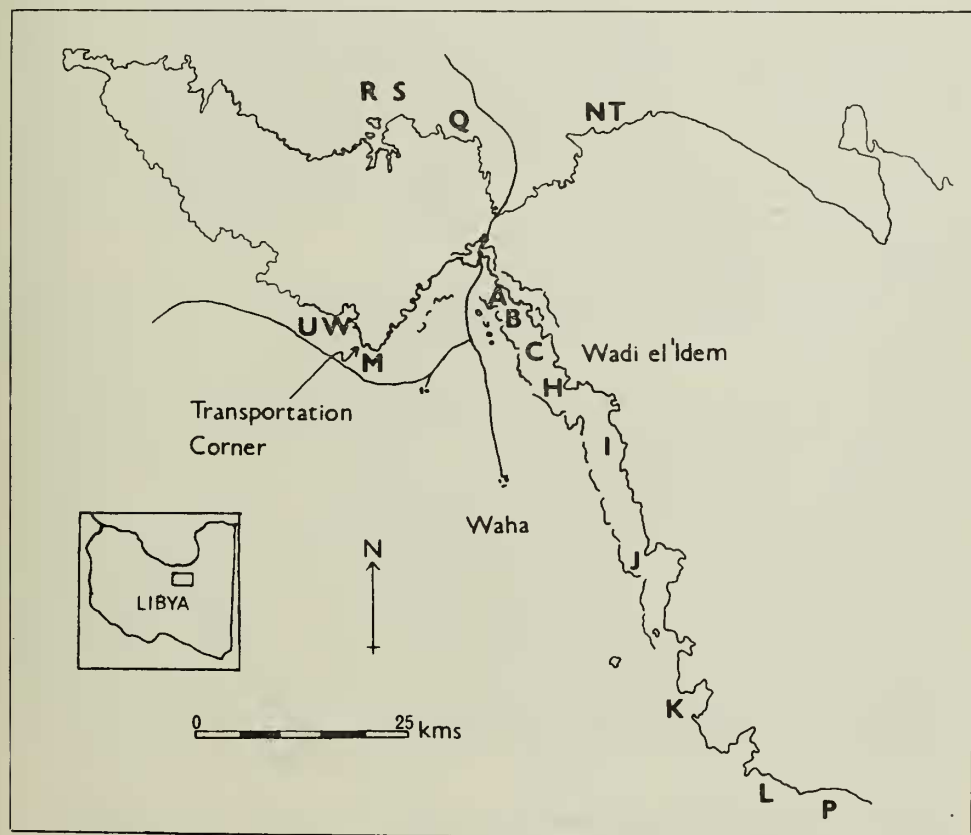


FIG. 1. Vertebrate localities of the Gebel Zelten.
Sites D, E, F and G are located between sites C and H.

The vertebrate fauna of the Gebel Zelten was discovered in 1958 by personnel of the Compagnie des Petroles Total (Libye) during a regional reconnaissance of Libya (Magnier, 1962). In December 1960 an expedition from the Museum National d'Histoire Naturelle, Paris, visited Gebel Zelten to exploit the vertebrate remains (Arambourg & Magnier, 1961). Only an area 20 km long at the centre of the northern scarp of the Gebel was prospected in detail but vertebrate specimens were collected from all exposures examined. The material retrieved is currently housed in the Institut de Paléontologie, Paris. A faunal list was given by Arambourg and Magnier (1961), and later revised by Arambourg (1963b). Of the elements listed only *Bunolistriodon massai* has been described in detail (Arambourg, 1963a) but preliminary descriptions of *Afrocyon burolleti*, *Prolibytherium magnieri*, *Mastodon pygmaeus* and an aeopyornithid tibia have been published (Arambourg 1961a, 1961b).

From 1964, expeditions from the University of Bristol under the leadership of Dr R. J. G. Savage have systematically collected vertebrate material from Gebel Zelten. Exploitation of the southern scarp was undertaken in 1964 and of the northern scarp in 1966. The 1967 and 1968 expeditions expanded and consolidated the results of earlier investigations. In all, well over a thousand specimens, representing several tons of unprepared material, have been collected by University of Bristol parties. This is in addition to the material collected by the 1960 French expedition and to the specimens donated by oil company personnel to the British Museum (Natural History) and American Museum of Natural History. A list of the faunal elements collected was given in Savage and White (1965) and revised in Savage (1967) and Selley (1968).

Most of the vertebrate fossils have been collected from channels and flood plains of the fluviatile facies, though remains are not infrequent in the tidal flat facies. At the time of writing 24 sites had been discovered and these were assigned letter prefixes in alphabetical order of discovery (see fig. 1). Permanent site numbers and other pertinent data are now on file in the Department of Geology, University of Bristol. All the Gebel Zelten sites occur near the base of the exposed section and range in areal extent from one to ten acres. A table showing the distribution of the Gebel Zelten mammal fauna by sites was given by Savage (in Selley, 1968).

Desio (1935) referred the rocks on the south side of the Gebel Zelten to the Aquitanian stage and those on the north scarp to the Burdigalian. The vertebrate fauna was allocated a Burdigalian age by Arambourg (1963b) although it is not clear whether this age was based on the mammalian elements or on the marine invertebrates. Savage and White (1965) confirmed a Burdigalian age for the mammals, and Savage (in Selley, 1968) later refined the age of the fauna to early Burdigalian or even late Aquitanian. Definite conclusions on the age of the Gebel Zelten assemblage must necessarily be delayed until all the mammalian groups represented have been thoroughly investigated. To date only the carnivores (Savage, 1973) and giraffoids (Hamilton, 1973) have been completed.

The Gebel Zelten deinotheres skulls are not only the earliest skulls, though not the earliest deinotheres specimens (which are from East Africa), but are also unusually complete. The best preserved specimen (6418 : 20) was collected in 1966 and was

deposited in the British Museum (Natural History). The accession number of the specimen is M.26665. All the permanent teeth are erupted and show wear but the zygomatic, squamosal, auditory and pterygoid regions are poorly preserved.

A virtually complete skull of an immature individual was collected by the writer from Site D in 1967. This specimen (6404 : 44) was completely buried and was only discovered during the excavation of deinother limb material, for which purpose site D had been revisited. The skull was lying on its side (the only deinother skull from Gebel Zelten that was not lying upside down) and had been slightly deformed by compaction after burial. The bone was in an extremely fragile state and the right zygomatic arch disintegrated during excavation. The occipital region fragmented and became partially deformed during transportation to Bristol. Permanent P³-M¹ are fully erupted but only M¹ shows wear. M² is only partly erupted. The squamosal, auditory and orbital regions are better preserved than in M.26665. Several of the facial sutures are still unfused. The mandible (6404 : 45) and much of the skeleton belonging to this individual (M.26667a-l) were excavated from the adjacent part of site D.

An incomplete deinother skull (6404 : 14) and much of a mandible (6404 : 13) were collected in 1964 from within a few yards of skull 6404 : 44. Unfortunately skull 6404 : 14 was broken in transit from the Gebel Zelten and only the premaxilla, jugal and dentition are now in a reasonable state of repair. The teeth of the 1964 specimens are in different stages of eruption and wear and are not thought to belong to one individual.

The 1968 Bristol expedition to Gebel Zelten and Dor el Talha discovered an incomplete and partly crushed skull at Gebel Zelten site L. Pieces of this skull were collected but all except a fragment of the inferior half of the occiput are still in Libya. The ventral edges of the lateral wings of the squamosal are better preserved on this specimen than on M.26665. Two other partly eroded skulls were discovered at site R by the 1966 expedition. These were allocated field numbers (6418 : 4, 6418 : 19) but have yet to be collected.

In addition to the deinother postcranial material from site D, a cuneiform and isolated vertebrae have been collected from other Gebel Zelten sites. Gebel Zelten deinother material is appreciably smaller than, and differs morphologically from, equivalent specimens of *Mastodon angustidens* from Gebel Zelten. In the ensuing descriptions, comparisons with recent elephant remains are based on vertebrae of *Loxodonta africana* from the British Museum (Natural History), the manus and pes of *L. africana* from the Osteology Department of the Centre for Prehistory and Palaeontology, Nairobi, and fore and hind limb material of *Elephas maximus* in the University of Bristol collections. Comparative deinother material includes the partial skeleton of '*Deinotherium bavaricum*' in the Naturhistorisches Museum of Vienna, the partial skeleton of *D. giganteum* from Valladolid in the Museo de Ciencias Naturales of Madrid, and carpals and tarsals of *D. giganteum* from Höwenegg in the University of Mainz collections.

Conclusions on deinother taxonomy, morphology and functional anatomy were made after viewing specimens in the following institutions: British Museum (Natural History), London; Centre for Prehistory and Palaeontology, Nairobi; Department

of Geology Museum, University of Bologna; Museo de Ciencias Naturales, Madrid; Institut de Paleontologie, Paris; Naturhistorisches Museum, Vienna; Institut für Paläontologie und Historisches Geologie, Munich; Hessisches Landesmuseum, Darmstadt; Naturhistorisches Museum, Mainz; Institut für Paläontologie, Johannes Wurtemberg Universität, Mainz; Naturhistorisches Museum, Wiesbaden. Extensive use has been made also of data given by Bergounioux & Crouzel (1962a, 1962b), Dehm (1963), de Pauw (1908), Graf (1957), McInnes (1942), Pacheco (1930), Palmer (1924), Sahni & Tripathi (1957), Stefanescu (1897, 1907), and Tobein (1962).

The results of these investigations suggest that some revision of deinotheres systematics is necessary. Diagnoses are given at the beginning of the section on systematic description because the Gebel Zelten deinotheres do not appear to belong to the type genus.

TABLE I

Deinotheres specimens from Gebel Zelten

Field number	Accession number	Description	Field number	Accession number	Description
6401 : 1		Left M ³	6404 : 47	M.26667i	Distal end of left humerus
6401 : 4		Right maxilla with P ³ -M ³	6405 : 98		Left cuneiform
6404 : 13		Mandible with tusks and cheek teeth	6409 : 41		M ² fragment
6404 : 14		Skull fragments with dentition	6410 : 2		Deciduous P ₄
6404 : 30	M.26667a	Distal end of fibula	6412 : 10		Tuskless mandible with worn cheek teeth
6404 : 31	M.26667b	Right ulna	6412 : 39		Left M ₂
6404 : 32	M.26667c	Proximal end of right humerus	6412 : 40		Left M ₁
6404 : 33	M.26667d	Right femur	6412 : 54		Left P ⁴
6404 : 34	M.26667e	Left ulna	6413 : 18		Left M ³
6404 : 36	M.26667f	Right scapula	6416 : 120		Tusk tip
6404 : 37	M.26667g	Left innominate	6416 : 130		Tusk
6404 : 38	M.26667h	Left rib head	6418 : 20		Adult skull
6404 : 39	M.26667i	Right neuropophysis of 3rd cervical vertebra	6418 : 22		Mandible with tusks and cheek teeth
6404 : 41	M.26667j	Proximal and distal end of left radius	6419 : 15		Atlas vertebra
6404 : 44		Immature skull	6419 : 16		Tusk alveoli
6404 : 45		Fragmented immature mandible	6419 : 17		Enamel fragment
6404 : 46	M.26667k	Distal end of right humerus	6421 : 2		Left M ²
			6421 : 15		Molar fragment
			6423 : 13		Enamel fragment
			6423 : 45		Enamel fragment
			6423 : 56		Enamel fragment
			**6424 : 79		Axis vertebra

** = Site unknown

III. SYSTEMATIC DESCRIPTIONS

Order PROBOSCIDEA Illiger, 1811

Suborder DEINOTHERIOIDEA, Osborn, 1921

Family **DEINOTHERIIDAE** Bonaparte, 1845

DIAGNOSIS. Large herbivorous graviportal mammals. Dental formula $\frac{0.0.3.}{1.0.2.3.}$ for the deciduous teeth and $\frac{0.0.2.3.}{1.0.2.3.}$ for the permanent dentition; DP_2^2 and P_3^3 with well developed external crest; DP_4^4 and M_1^1 trilophodont; the remainder of the cheek teeth are bilophodont. Horizontal tooth replacement not developed so that all permanent teeth may be erupted at the same time (cf. elephantoids). Mandibular symphysis and lower tusks curved downwards so that the tusk tips are vertically or nearly vertically aligned. Skull low with deep rostral trough, retracted external nares, low orbit, inclined occiput, high occipital condyles, elongate paroccipital processes, and diplöe.

MIOCENE	PLIOCENE	PLEISTOCENE	
	<i>P. hobleyi</i>		AFRICA
		<i>D. bozasi</i>	
<i>P. bavaricum</i>			EUROPE
	<i>D. giganteum</i>		
<i>P. pentapotamiae</i>			ASIA
	<i>D. indicum</i>		

FIG. 2. Temporal and geographic distribution of deinotheriid taxa.

REMARKS. The family Deinotheriidae originated in Africa. The earliest and most primitive forms are from East African localities of early Miocene age. During the Burdigalian the early representatives of this family migrated into Asia and Europe. By the middle of the Miocene epoch, larger and more advanced representatives had appeared in Europe and Asia. The primitive and advanced forms coexisted until the end of the Miocene in Asia and the end of the Pontian in Europe. The more advanced forms lingered on until the middle Pliocene in Eurasia. Only the early and primitive form is known from the Neogene of Africa; a larger and more advanced form occurred in the Pleistocene but the two forms are not known to have coexisted.

Deinotheriid species have been commonly allocated to a single genus—*Deinotherium*—erected by Kaup in 1829. The species were defined upon geographic distribution and characters of the mandible and dentition. While the cheek teeth exhibit a great deal of variation in cusp morphology from specimen to specimen, these differences do not readily lend themselves to species differentiation, especially when the several species are interpreted as belonging to a single genus. Moreover the concept of a single deinotheres genus does not adequately express the fundamental division of the family into an early and primitive group of species (*D. hobleyi*, *D. bavaricum* and *D. pentapotamiae*) and a later, more advanced group (*D. giganteum*, *D. indicum* and *D. bozasi*). The recent discoveries of deinotheriid skull and postcranial material, coupled with the re-examination of well documented specimens confirms that the two groups of deinotheres may be separated morphologically. It would appear therefore that division of the family into two genera is warranted. This idea was originally put forward by Ehik (1930) but has subsequently been ignored. On evidence currently available, however, Ehik's premise is substantiated. The two genera are defined below.

Genus *Deinotherium* Kaup, 1829

REVISED DIAGNOSIS. Large deinotheres. Dental formulae as for the family; tendency for the development of subsidiary styles on P^{3-4} and for simplification of the postmetaloph ornamentation of M^{2-3} when compared to *Prodeinotherium*. The skull rostrum not parallel to the mandibular symphysis and nearly horizontally aligned; rostral trough and external nares wide; preorbital swelling sited anteriorly on the rostrum; skull roof short and narrow at the temporal fossae; occiput slopes gently posteriorly; occipital condyles elevated above the level of the external auditory meatus; paroccipital processes very elongate. Postcranial skeleton with cursorial modifications to graviportal structure; scapular spine reduced with no acromion or metacromion; carpals and tarsals narrow with dolichopodous metapodials exhibiting functional tetradactyly.

REMARKS. Most of the diagnostic characters of *Deinotherium* concern the skull and postcranial characters. The teeth, however, are the most commonly preserved remains. Teeth that may be attributed to *Deinotherium* are almost always larger than the equivalent teeth of *Prodeinotherium*. Both genera exhibit a tendency to increase in size through geologic time, and in Europe there is an overlap in absolute size of the cheek teeth of the two genera. This is due to the greater numbers and greater longevity of deinotheres specimens from that continent, but at any one horizon the teeth of *Deinotherium* are always unmistakably larger than those of *Prodeinotherium*. On the basis of specimens examined and of those reported by Graf (1957), McInnes (1942) and Sahni & Tripathi (1957), the *minimum* parameters of *Deinotherium* teeth would appear to be as follows:

Tooth	Length (in mm)	Breadth (in mm)
P ³	63	55
P ⁴	59	62
M ¹	71	64
M ²	70	74
M ³	70	74
P ₃	51	43
P ₄	61	48
M ₁	74	54
M ₂	73	63
M ₃	75	65

These parameters agree well with those noted by Bergounioux & Crouzel (1962a) who also define parameters for the deciduous teeth.

TYPE SPECIES. *Deinotherium giganteum* Kaup, 1829 (including *D. gigantissimum* Stefanescu, 1897).

OTHER RECOGNISED SPECIES: *D. indicum* Falconer, 1845; *D. bozasi* Arambourg, 1934.

A detailed synonymy of *D. giganteum* was given by Graf (1957) and of *D. indicum* by Sahni & Tripathi (1957).

Genus *Prodeinotherium* Ehik, 1930

REVISED DIAGNOSIS. Small deinotheres. Dental formulae as for the family; M²⁻³ with well defined postmetaloph ornamentation. Skull rostrum turned down parallel to the mandibular symphysis; rostral trough and external nares narrow; preorbital swelling close to orbit; external nares anteriorly sited and nasal bones with anterior median projection; skull roof relatively longer and wider than in *Deinotherium*; occiput more vertically inclined; occipital condyles sited more ventrally than in *Deinotherium* and level with the Frankfurt Plane; paroccipital

processes short. Postcranial skeleton graviportally adapted; scapula with well defined spine and stout acromion and metacromion; tarsals and carpals narrow but not dolichopodous.

REMARKS. This genus was originally proposed by Ehik (1930) for a small species of deinothere from Kotyhaza, Hungary. The Kotyhaza specimens comprised a jaw, some teeth, and a few incomplete limb elements. These specimens were generally smaller than is normal in *D. bavaricum* but were subsequently attributed to this taxon without objection (Graf, 1957; Bergounioux & Crouzel, 1962a; etc.). I agree that the taxa *bavaricum* and *hungaricum* are probably conspecific but propose to allocate them to *Prodeinotherium*. Ehik's generic taxon is therefore resurrected to encompass the small, early and primitive species of deinothere from the Neogene of Africa and Eurasia. The slight change in spelling from *Prodinotherium* (Ehik, 1930) to *Prodeinotherium* is, in view of Kaup's spelling of the type genus of the family Deinotheriidae, considered to be a justifiee emendation according to the International Code of Zoological Nomenclature (Stoll *et al*, 1961) section 9, article 50, paragraph (c).

Specimens that may be attributed to species of *Prodeinotherium* are observed to increase in size through geologic time. The *maximum* parameters for the permanent cheek teeth of *Prodeinotherium*, based on personal observation and data from Graf (1957), McInnes (1942), and Sahni & Tripathi (1957) are as follows:

Tooth	Length (in mm)	Breadth (in mm)
P ³	63	60
P ⁴	61	62
M ¹	73	69
M ²	73	75
M ³	69	72
P ₃	51	43
P ₄	60	52
M ₁	73	53
M ₂	75	70
M ₃	81	68

Similar figures are given by Bergounioux & Crouzel (1962a) who also define size limits for the deciduous teeth.

TYPE SPECIES. *Prodeinotherium bavaricum* (von Meyer), 1831.

OTHER RECOGNIZED SPECIES. *P. pentapotamiae* (Falconer), 1868; *P. hobleyi* (Andrews), 1911.

A detailed synonymy of *P. bavaricum* was given by Graf (1957) and of *P. pentapotamiae* by Sahni & Tripathi (1957).

TABLE 2

Comparison of *Prodeinotherium* and *Deinotherium*

	<i>Prodeinotherium</i>	<i>Deinotherium</i>
<i>Skull.</i>	rostrum ventrally flexed rostrum narrow and deep preorbital swelling close to external nares external nares almost as deep as wide external nares surmounted by median projection of nasals orbit above P ³ skull roof nearly flat and inclined anteriorly occiput steeply inclined paroccipital processes longer than in elephantoids occipital condyles cut ventrally by Frankfurt Plane	rostrum almost straight rostrum wide and shallow preorbital swelling more anteriorly sited external nares much wider than deep no median projection of nasals orbit above P ⁴ skull roof shorter and narrower at the temporal fossae occiput gently inclined paroccipital processes longer than in <i>Prodeinotherium</i> occipital condyles elevated above Frankfurt Plane
<i>Dentition.</i>	P ³⁻⁴ usually lack mesostyles M ²⁻³ with well developed postmetaloph ornamentation tusks nearly vertical	P ³⁻⁴ often possess mesostyles M ²⁻³ with reduced postmetaloph ornamentation tusks longer and may be recurved beneath symphysis
<i>Skeleton.</i>	scapula—stout spine, metacromion and acromion; supraspinous fossa well developed humerus—lateral epicondyle tapers proximally radius—medial half of head larger than lateral half; distal epiphysis more massive than in <i>Mastodon angustidens</i> lunar—radial facet covers most of proximal surface; magnum facet is concavo-convex cuneiform—posterolateral process of similar length to that of <i>Elephas</i> but does not articulate with unciform; unciform facet is concavo-convex unciform—cuneiform facet roughly triangular; largest distal facet is for McV magnum—proximal surface has large posteromedial projection metacarpals—laterally compressed but of similar size to <i>Mastodon angustidens</i> manus more plantigrade femur—similar length to <i>Elephas maximus</i> astragalus—tibial facet equant and convex; prominent posteromedial process	scapula—reduced spine and no metacromion or acromion; supraspinous fossa greatly reduced humerus—lateral epicondyle does not taper proximally radius—medial half of head correspondingly larger; distal epiphysis more massive than in <i>Prodeinotherium</i> lunar—radial facet extends less far posteriorly; magnum facet almost flat cuneiform—posteriolateral process is relatively longer and more ventrally inclined than in <i>Prodeinotherium</i> ; unciform facet is biconcave unciform—cuneiform facet extends farther posterolaterally and distally, and tapers more abruptly posteriorly; largest distal facet is for McIV magnum—posteromedial projection is less pronounced metacarpals—more compressed laterally and distinctly more elongate than in <i>Prodeinotherium</i> manus more digitigrade femur—proportionately 30% shorter than in <i>E. maximus</i> astragalus—tibial facet equant but nearly flat posteromedial process more reduced than in <i>Prodeinotherium</i>

Teeth are the most common deinotheres remains, but although there is a great deal of variation in minor topographic features on the cheek teeth the basic tooth morphology is conservative throughout the known history of the group. Indeed, when only a single genus—*Deinotherium*—was accepted, tooth morphology was of far less importance for specific differentiation than absolute size of the teeth or geographic distribution of the specimens. In effect only two distinct species could be recognized—*D. giganteum* and *D. bavaricum*. However, with these two taxa separated by generic rank, tooth morphology assumes greater diagnostic importance. It is entirely possible that detailed revision of known material will furnish evidence for distinguishing different lineages within the two genera incorporating variations in cheek tooth morphology. Such a revision is, however, beyond the scope of this paper.

Only two deinotheres species are currently recognized from fossil mammal sites in Africa—*Prodeinotherium hobleyi* of the Neogene and *Deinotherium bozasi* of the Quaternary. The Gebel Zelten deinotheres teeth are more advanced than specimens of *P. hobleyi* from the earliest Miocene of East Africa but more primitive than those from Ngorora (Pliocene) in Kenya. The observed differences are insufficient at present to warrant the erection of a separate taxon for the Libyan material.

Prodeinotherium hobleyi (Andrews), 1911

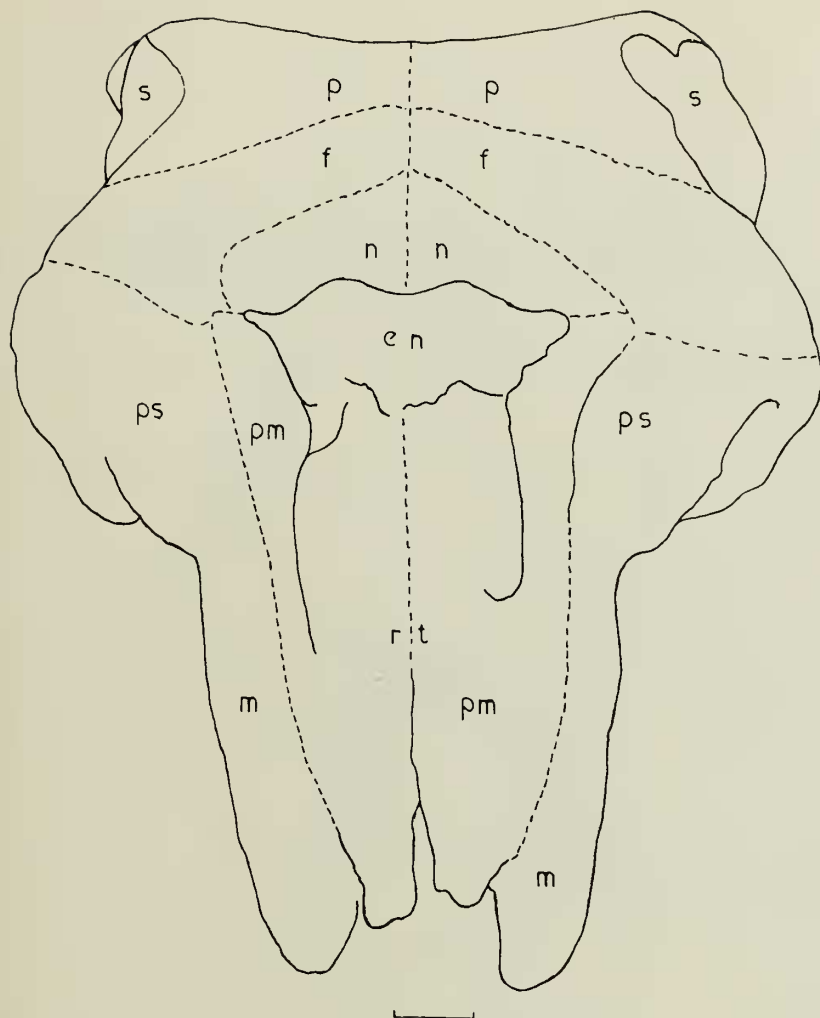
- 1911 *Deinotherium hobleyi* Andrews: 943.
 1919 *Deinotherium cuvieri* Kaup; Brives: 90.
 1957 *Deinotherium bavaricum* v Meyer; Graf: 152.
 1967 *Deinotherium cuvieri* Kaup; Savage: 263.

Skull

(Text-figs 3–6; Plates 1–3)

MATERIAL REFERRED. 6404 : 14, fragmentary adult skull with only the dentition, right premaxilla, left jugal and occipital condyles well preserved; 6404 : 44, complete but slightly distorted immature skull; M.26665, virtually complete skull but with zygomatic arches, squamosal, auditory and pterygoid regions poorly preserved; 6418 : 4 and 6418 : 19, incomplete and uncollected skulls.

DESCRIPTION. The skull of *Prodeinotherium hobleyi* from Gebel Zelten is elongate and low, the length of the cranium being twice that of the rostrum. The skull is characterized by a relatively flat skull roof which ascends gently to the lambdoidal crest, a small orbit that is open posteriorly, a broad and downturned rostrum that is surmounted by massive preorbital swellings, high occipital condyles, and a backwards sloping occipital region. The rostrum is appreciably narrower than in *Deinotherium giganteum* and is excavated to form a deep rostral trough anterior to the external nares. The occipital region is very wide owing to the well developed lateral wings of the squamosal bones. Much of the skull is formed from cancellous bone, and where the surface bone has been eroded diplöe similar to those of elephantoid skulls may be detected.



Key to letters used in text-figures 3, 4, 5 & 6.

b = auditory bulla
 en = external nares
 f = frontal
 fo = foramen ovale
 fr = foramen rotundum
 ga = glenoid articulation surface
 in = internal nares
 io = infraorbital foramen
 lc = lamboidal crest
 ls = lateral wing of squamosal
 m = maxilla
 n = nasal
 ns = nasal sinus
 o = orbit

oc = occipital condyle
 p = parietal
 pf = posterior palatine foramen
 pgf = postglenoid fossa
 plf = posterior lacerate foramen
 pm = premaxilla
 po = postorbital process of frontal
 pp = paroccipital process
 ps = preorbital swelling of maxilla
 pt = pterygoid process
 rt = rostral trough
 s = squamosal
 tf = temporal fossa
 zm = zygomatic process of maxilla
 zs = zygomatic process of squamosal

FIG. 3. *Prodeinotherium hobleyi* skull, anterior view. Scale = 5 cm.

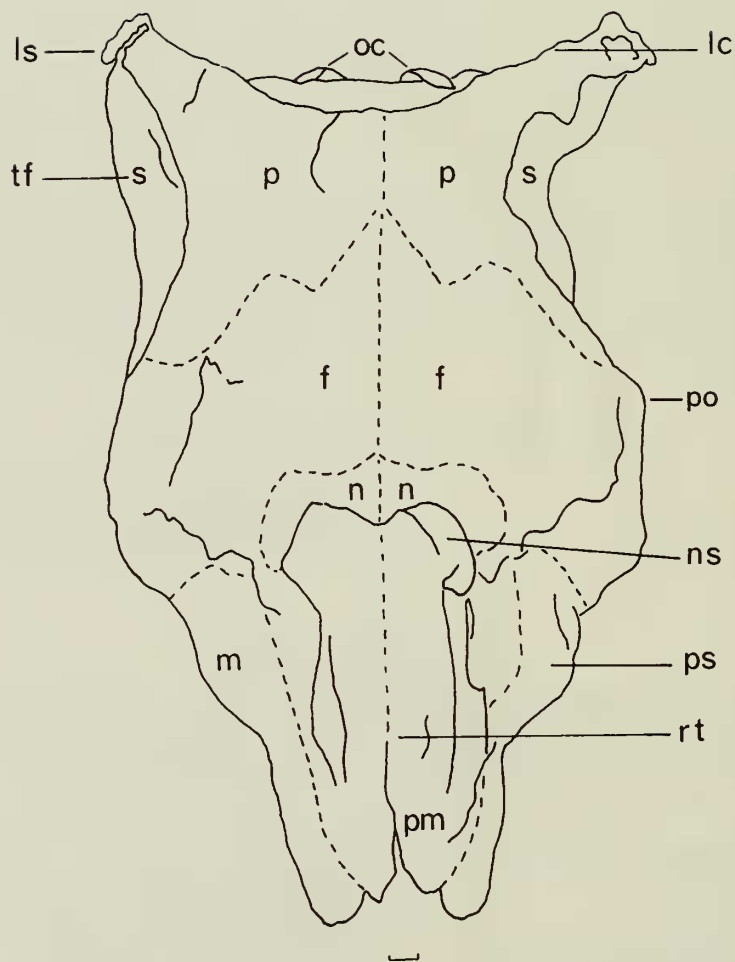


FIG. 4. *Prodeinotherium hobleyi* skull, dorsal view. Scale = 5 cm.

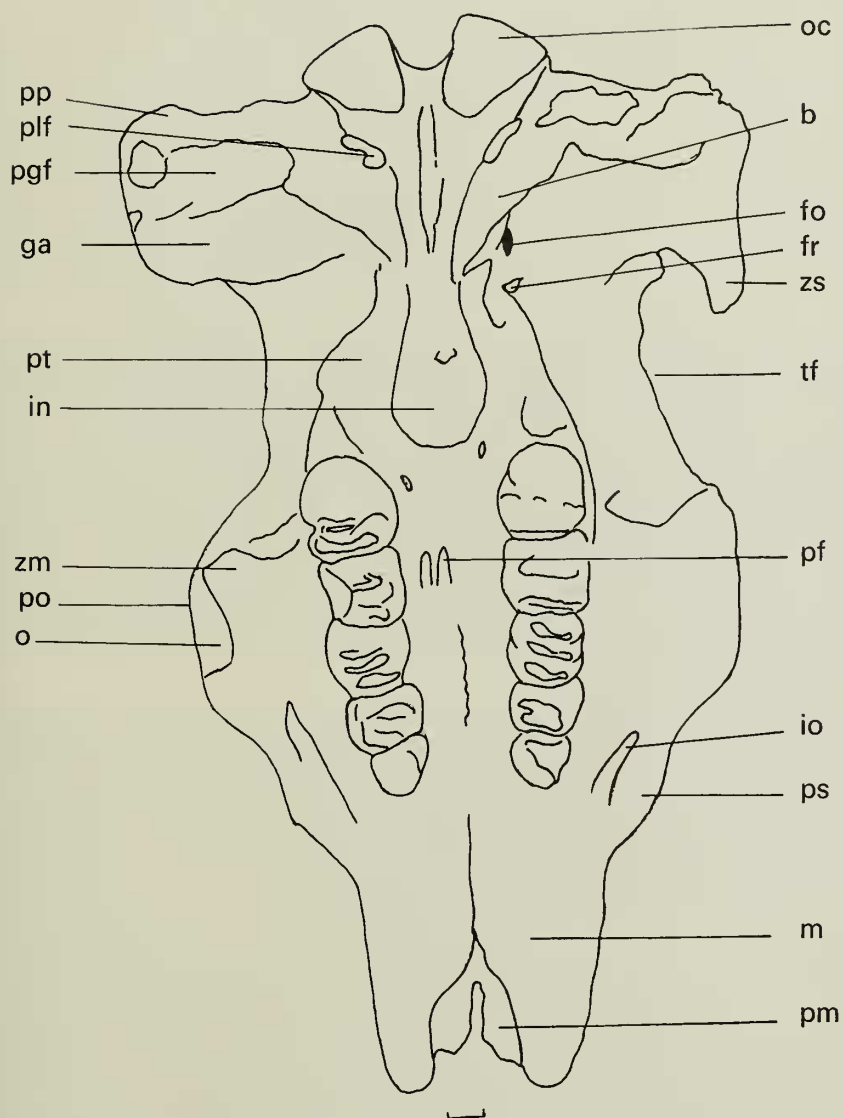


FIG. 5. *Prodeinotherium hobleyi* skull, ventral view. Scale = 5 cm.

Premaxilla. The dorsal surface of the deep rostral trough (text-figs 4, 5) anterior to the external nares is lined by the premaxillae. The anterior portion of the premaxilla forms a small flange projecting anteriorly from the upstanding rugose walls of the rostral trough (Pl. 1a). The premaxillary-maxillary suture extends from the lateral edge of this flange along the medial edge of the wall of the rostral trough until it meets the anterior wing of the nasal (text-figs 3, 4). The suture has completely fused in skull M.26665 but the premaxillary-maxillary contact is denoted by the junction of smooth bone, typical of the medial walls and floor of the trough, with the rugose bone of the lateral walls and dorsal surface. The suture is still visible in skull 6404 : 44. The posterior limit of the premaxilla beneath the external nares is not clear owing to the fusion of sutures in M.26665 and the cracked nature of the bone in 6404 : 44. Perhaps the limit is marked by the anterior edge of the cavernous nasal sinus (text-fig. 4, Pl. 1b) that occurs on either side of the external nares.

Viewed from the dorsal aspect, each premaxilla is roughly triangular with the posterior edge of the bone forming the shortest side. In transverse section the distal part of the premaxilla is L-shaped, the ascending arm lining the medial wall of the rostral trough while the body forms the floor. Medial to the preorbital swelling of the maxilla (text-figs 3, 4, 5; Pls. 1-2), the ascending process of the premaxilla bulges medially in front of the nasal sinus, and here the surface of the bone is curved sigmoidally. The facial process of the premaxilla ascends to contact both the nasal and the anteriormost prolongation of the frontal bone (text-figs 3, 4), thereby excluding the maxilla from contact with the nasal. Ventrally the premaxilla is visible only at the anterior third of the rostrum where the premaxillary flanges appear above the diverging tips of the maxillae (text-fig. 5; Pl. 3b). The flanges of the premaxillae converge ventrally.

Maxilla. This is the largest bone of the facial region, extending from the dental alveoli up to the level of the external nares, and from the anterior tip of the rostrum to behind the dentition. The facial process of the maxilla is contiguous with the frontal, lacrimal and premaxilla. It continues forwards and downwards from the orbit as the external wall of the rostral trough. Just anterior to the frontal-maxillary suture the dorsal and dorsolateral parts of the rostral walls are swollen in skull M.26665 to form a massive preorbital swelling. In 6404 : 44 the swelling is less pronounced but this portion of the maxilla is considerably elevated above the remainder of the dorsal rim of the rostral trough. The infraorbital foramen (Pl. 2a and b) is large and the anterior opening lies above the anterior edge of the third premolar. In skull M.26665 two deep grooves extend anteriorly from the infraorbital foramen. One runs for a short distance down the lateral surface of the rostrum; the other extends parallel to the dentition to terminate on the dorsal surface of the rostral trough immediately in front of the preorbital swelling. These grooves mark the proboscideal branches of cranial nerves V and VII. In skull 6404 : 44 only the former groove is well developed. The jugal process of the maxilla is stout, expanding posteriorly to define the posteroventral limit of the orbit (Pl. 2a). The posterior opening of the infraorbital canal is sited above the base of the jugal process of the maxilla and beneath the postorbital process of the frontal (Pl. 2b).

In ventral aspect the maxillae diverge behind the anterior third of the rostrum, revealing the margins of the premaxilla. Behind the anterior third of the rostrum the intermaxillary suture extends posteriorly down the midline of the palate as a cristiform ridge (Pl. 3b). The maxillary-palatine suture is fused in skull M.26665 but is presumed to have been level with the posterior root of the second molar and to have incorporated the paired posterior palatine foramina. Shallow grooves extend anteriorly from these foramina until level with the fourth premolars. The lingual border of the alveolar region is continued forward from the anterior root of the premolar as a broad, rounded ridge, converging on its fellow towards the tip of the rostrum. On the medial side of this ridge a very weak crest extends anteriorly to meet the ventral exposed portion of the premaxilla. The plate is vaulted in the vicinity of the premolars and narrows as it continues forwards beneath the rostrum. In the region of the molars the palate is convex.

Nasal. In skull M.26665 the nasal-frontal suture is fused but there is a pronounced break of slope some 7 cms behind the external nares that probably indicates the junction of these bones. The surface of the bone immediately above and behind the external nares is much smoother than the adjoining bone. In 6404 : 44 the lateral wing of the nasal extends laterally until level with the front of the orbit and the suture with the premaxilla is well defined. In dorsal plan the nasals are crescentic (text-fig. 4). In M.26665 the nasals continue anteriorly at the intranasal suture to form a well developed median projection (Pl. 1a and b) though this is less well developed than that of the extant elephants. In 6404 : 44 the anterior portion of the intra-nasal suture is marked by an indentation rather than by a projection; this is attributed to the relative immaturity of the specimen. Apparently the nasal bones do not contribute to the cavernous nasal sinuses on either side of the external nares.

Lacrima. Due to fusion of the sutures and to incomplete preservation the lacrimal is not well delineated in skull M.26665 but in 6404 : 44 the lacrimal is seen to form the anteroventral quadrant of the rim of the orbit. The lacrimal bone is triangular with the base of the triangle elevated a short distance above the infra-orbital canal. From the centre of the ventral half of the bone a lacrimal foramen opens into a lacrimal canal that passes outwards to the anteroventral rim of the orbit. Above the lacrimal foramen is a large traction epiphysis. The lacrimal is contiguous only with the frontal and maxilla and does not form part of the infra-orbital swelling of the maxilla (cf. Andrews, 1921; 530).

Jugal. This bone is missing from skull M.26665 but is known from 6404 : 44 and from the incomplete skull 6404 : 14. The jugal joins the zygomatic process of the maxilla at the posteroventral edge of the orbit, at which point the zygomatic process of the maxilla attains its greatest height. From the vertical jugal-maxillary suture the jugal increases in height posteriorly while simultaneously becoming flattened from triangular to oval in transverse section. The posterior portion of the jugal is overlapped by the zygomatic process of the squamosal. The posterior end of the jugal forms a smooth convex curve and gives off a small conical process from the posterior ventral surface. A jugal from skull 6404 : 44 is less massive and lacks the conical process on the posterior ventral surface.

Palatine. This is fused to the palatine process of the maxilla level with the posterior root of M² and extends for some distance behind M³. The palatine is pierced by two asymmetrically placed posterior palatine foramina. In M.26665 the anteriormost part of the palatonarial border is sited some way behind M³ and is gently curved with the lateral, more posterior, portions missing. The internal narial opening is almost circular.

Vomer. The vomer extends back behind the level of the anterior part of the palatonarial border and forms a V-shaped crest along the roof of the internal nares. Immediately above the posterior end of the vomer a small chip of bone is missing in skull M.26665 thus revealing part of the cavernous ethmoidal fossa.

Frontal. In M.26665 the frontal bones occupy just over half of the skull roof (text-fig. 4). The nasal-frontal suture is fused but the anterior edge of the frontals may be determined as above. Part of the frontal-parietal suture is revealed in the centre of the skull roof of M.26665 as a sinuous interdigitating groove but this cannot be traced laterally. The frontals are slightly domed convexly in the midline and over the large postorbital processes. There are no supratemporal ridges. Both the frontal and parietal portions of the skull roof extend ventrally to contribute to the temporal fossa. The postorbital processes of the frontals (text-fig. 4) are blunt protruberances from each of which a ridge descends ventrally and posteriorly to continue as the free end of the alisphenoid. In front of these processes the frontals demarcate the upper rim of the orbit.

Parietal. The parietal bones form the posterior part of the skull roof. They increase in width anteriorly from the lambdoidal crest. The lambdoidal crest forms the most elevated portion of the skull roof and strongly delineates the latter from the occipital region. The dorsal surface of the parietals is slightly concave in transverse section and there is no sagittal crest.

Fusion of the sutures on the posterior half of the cranium makes the boundary of the parietals indistinct. Even in the immature skull (6404 : 44) the junctions of the parietals, squamosals, alisphenoids and frontals are not clear. Beneath the sharply delineated rim of the temporal fossa the bone in M.26665 is sculpted by deep and wide grooves denoting the point of attachment of the temporal muscle. Ventral to the sculpted surface the bone is much cracked and broken. In 6404 : 44 the walls of the temporal fossae are better preserved but the bone shows no temporal muscle scars. No trace of an interparietal may be detected.

Supraoccipital. This contributes to the central and dorsal regions of the occiput (Pl. 3a) and is concave both sagittally and transversely. The perimeter of this bone is fused but it must have been roughly triangular; whether or not it formed the dorsal border of the foramen magnum cannot be determined. The dorsal edge contributes to the posterior side of the central portion of the lambdoidal crest. The lateral junction with the squamosal may be indicated by a pronounced ridge that extends from the paroccipital process to the lambdoidal crest. The supraoccipital is excavated in the midline by two deep triangular pits that form fossae for the nuchal ligament. The dorsal edge of the nuchal fossa lies some 5 cms below the lambdoidal crest; the ventral edge some 8 cms above the foramen magnum. As in elephantoid skulls, the two halves of the nuchal fossa are separated by a narrow ridge of bone. The floor

of each pit is comprised of sculpted bone, as is that region between the top of the nuchal fossa and the lambdoidal crest.

Exoccipital. The paired exoccipital bones form the ventrolateral regions of the occiput and support very large and prominent occipital condyles. From the dorsolateral edge of the nuchal fossa of skull M.26665 a prominent crest curves ventrally and laterally to terminate on the lateral edge of the paroccipital process. This ridge is interpreted as separating the exoccipital from the lateral wing of the squamosal and is continuous with the lateral limit of the supraoccipital. The condyles are triangular and converge as they taper ventrally. The condyles are limited ventrally by a deep groove (the condyloid fossa of Palmer, 1924) that is also present, though less prominent, on the dorsal edge. The condyles are most elevated from the rest of the exoccipital bone at their anteromedial edge at which point they protrude almost at right angles from the plane of the occiput. The paroccipital processes are incomplete on M.26665 but on 6404 : 44 are seen to extend for some distance below the base of the occipital condyles, merging laterally with the ventral edge of the lateral wing of the squamosal.

Basioccipital. Fusion of the sutures and incomplete preservation prevents delineation of the periphery of this bone in M.26665. The basioccipital descends steeply from the foramen magnum and becomes progressively more narrow anteriorly (text-fig. 5; Pl. 3b). The posterior part is deeply notched by the foramen magnum and extends laterally to the medial edges of the occipital condyles. Anteriorly and ventrally the body is keeled. The anteroventral junction with the basisphenoid is probably level with the glenoid articulation surface. The basisphenoid passes uninterruptedly from the basioccipital but the keel becomes less pronounced anteriorly and disappears before reaching the internal narial opening.

The basicranium of 6404 : 44 has been distorted by crushing and the ventral surface is now parallel with the left lateral side. Slightly anterior to, and on either side of, the notch excavated by the foramen magnum is a large boss. This probably served for the insertion of the rectus anticus muscles. The right boss is level with, but somewhat below, the paroccipital process. The left boss is less well preserved. From this point the basioccipital narrows appreciably as it continues anteriorly. Some 5 cms in front of the anterior edge of the foramen magnum a pronounced keel extends down the midline. This keel extends for at least 9 cms until level with the eustachian opening of the auditory bulla but in front of this point the bone is too badly displaced to allow further observation of the keel. On either side of the posterior end of the keel are excavated large fossae for insertion of the rectus anticus major muscles. An elongate notch, the posterior lacerate foramen, is sited anterior to the paroccipital process and lateral to the basioccipital at the posterior end of the keel.

Sphenoid. The junctions of the various component parts of this bone with each other and with contiguous elements are for the most part indistinct. The anterior boundary of the alisphenoid forms part of the prominent cristiform outer wall of a deep groove that extends from the pterygoid process to the postorbital process of the frontal. The optic foramen, that probably perforated the orbitosphenoid, lies some distance above and anterior to the slit-like anterior lacerate foramen, and the orbitosphenoid-alisphenoid suture undoubtedly lay somewhere

between the two. Both foramina lie in a deep groove beneath the alisphenoid-frontal ridge. From the optic foramen a shallow groove extends forwards to the orbit, marking the course of the optic nerve. The foramen rotundum lies posterior to the anterior lacerate foramen and opens from the alisphenoid flap into a large alisphenoid canal. The mandibular branch of the fifth cranial nerve emerged from the posterior opening of the alisphenoid canal while the facial and maxillary branches emerged from the anterior opening. The position of the maxillary branch is marked by a deep groove, partly covered by a flap of bone, that extends towards the pterygoid process. In skull M.26665 this groove extends almost vertically (Pls. 2a and b) but in 6404 : 44 it passes anteriorly at an angle of 45° . Behind the posterior exit of the alisphenoid canal, and above the anterior portion of the auditory bulla, is a large foramen ovale (text-fig. 6).

The pterygoid region is very poorly preserved in skull M.26665. Ventrally and medially it passes uninterruptedly into the presphenoid and posteriorly into the alisphenoid. Nearly all of the ventral part that, together with the palatine, forms the lateral border of the internal nares is missing. The posterior surface of the pterygoid forms a smooth crest that passes laterally to the anterior tip of the petrosal. This region is also poorly preserved in skull 6404 : 44.

Squamosal. This is one of the largest bones of the skull and forms the postero-ventral wall of the temporal fossa. It is only poorly preserved in M.26665 and in many places the surface bone is missing to reveal diplöe beneath. The squamosal continues anteriorly and laterally from the supraoccipital to project as a vast lateral wing forming the widest part of the skull (text-fig. 4; Pl. 1b). The external edge of this wing passes uninterruptedly from the lambdoidal crest into the paroccipital process of the exoccipital. In lateral aspect the junction of the squamosal with both the alisphenoid and the parietal is indistinct. The zygomatic process of the squamosal is less stout than that of the maxilla, being almost quadrate in transverse section near the point of origin but becoming more slender as it extends forward

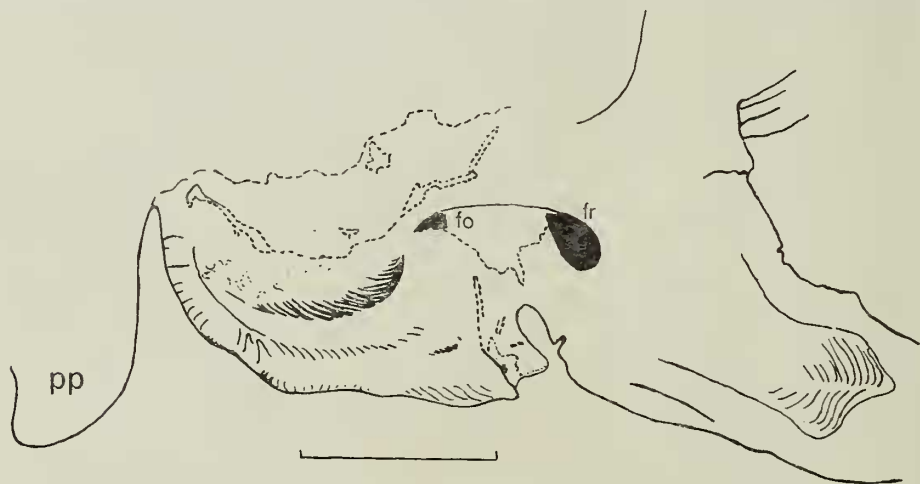


FIG. 6. *Prodeinotherium hobleyi* right auditory bulla. Scale = 5 cm.

to overlap the jugal. The auditory meatus opens onto the external surface of the lateral wing immediately posterior to, and slightly above, the zygomatic process. In M.26665 this region is poorly preserved but in 6404 : 44 the passage of the meatus is clearly seen. The passage of the meatus is gently inclined medially. The glenoid articulation surface is convex and elongate transversely. There is no postglenoid process and behind the glenoid surface there is a shallow transverse channel forming the floor of the auditory meatus as in *Elephas*.

Tympanic bulla. The tympanic bullae are incompletely preserved in M.26665 but are seen to be relatively larger than in the skull of *D. giganteum* from Eppesheim, Germany. Much of the surface bone on the Gebel Zelten specimen is missing and sufficient detail is preserved to show only the eustachian opening below and behind the foramen ovale. In skull 6404 : 44 both bullae are present but the left bulla is incomplete and crushed and the right bulla (text-fig. 6) is incomplete. The bullae are bounded medially by the basioccipital and basisphenoid (contributing in part to the posterior lacerate foramen), posteriorly by the paroccipital process, and dorsally by the squamosal and alisphenoid. The bulla projects ventrolaterally as a semi-circle of bone. In dorsal aspect it may be divided into two unequal portions—a posterior concave surface and an anterior (slightly larger) convex area. The regions are separated by a ridge that runs posteriorly and laterally from the foramen ovale to merge with the lateral perimeter level with the posterior lacerate foramen. The concave area thus enclosed presents an irregular surface pitted with numerous small foramina. The anterior portion of the dorsal surface is convex and consists mainly of smooth bone although it is pierced by several small foramina and canals near the anterolateral edge. The eustachian opening occurs at the anteromedial tip.

On skull 6404 : 44 the ventral surface of both bullae is incomplete but sufficient bone is preserved to permit a composite description. The ventral surface is divided sagittally into two unequal portions by a crest that extends from the paroccipital process to the anterolateral margin of the bulla. The portion of the bulla lateral to the crest is the smaller. The ridge is most pronounced posteriorly where it separates the posterior lacerate foramen from the large stylomastoid foramen, and becomes progressively less distinct anteriorly. The bone anterior to the stylomastoid foramen and lateral to the ridge is concave transversely and heavily sculpted. This part of the bulla is equivalent to the tympanohyal pit. Medial to the crest the surface of the bulla is smooth but cut by transverse shallow grooves. This portion of the left bulla is crushed and fragmented; on the right bulla the surface bone is missing from the anteromedial region to reveal the cavernous tympanum. In comparison with that of the extant elephants, the tympanic bulla of *Prodeinotherium* is less elongate sagittally and wider transversely with a larger stylomastoid foramen.

OTHER DEINOTHERIID SKULLS. *Prodeinotherium pentapotamiae*. An incomplete skull of *P. pentapotamiae* was collected in 1912 by Pilgrim from the Lower Chinji Sandstone, four miles from Chinji in the Salt Range of India. Two portions of the skull are preserved—a palate with cheek teeth (I.M. A.460) and a basicranium (I.M. A.461). These are of similar size to those of the Gebel Zelten skulls and were

described by Palmer (1924). The skull foramina that Palmer identified are sited similarly to those of the Gebel Zelten skulls. Only the base of the vertical tapering pillar that Palmer identified as the hyoid is still preserved but the basal tympanohyal portion would have fitted well into the elongate and narrow tympanohyal pit anterior to the stylomastoid foramen in Gebel Zelten skull 6404 : 44. Unlike Palmer, I do not believe that the right paroccipital process of the Indian skull can be far from its original position. Palmer had correctly identified the tympanic bullae, unlike Andrews (1921), but these are now only poorly preserved on the Indian specimen.

Eppelsheim skull. The skull of *Deinotherium giganteum* from Eppelsheim, Germany, was originally described by Klipstein and Kaup (1836) and the most recent description of this specimen was given by Andrews (1921). In the light of the information provided by the Gebel Zelten *Prodeinotherium* material it is now necessary to revise some of Andrews' interpretations of the Eppelsheim specimen. For example, on page 527 Andrews remarks:

' . . . de Blainville suggests that possibly the occipital surface had been crushed down towards the floor of the skull. Careful examination of the specimen, however, does not seem to support this idea and it seems probable that . . . it represents the condition of the living animal.'

TABLE 3

Prodeinotherium hobleyi skull measurements

<i>Parameter</i>	M.26665	6404 : 44
Total length of skull	94	73
Width anterior tip of rostrum	13.6	10.1
Length rostrum to external nares	42	34
Width skull at external nares	53	38
Width rostral trough at external nares	17.8	11.8
Length external nares to lambdoidal crest	40	31
Minimum width skull roof	42	28
Width lambdoidal crest	59.6	35
Height foramen magnum to lambdoidal crest	25.4	—
Height nuchal fossa	12.3	12.6
Width nuchal fossa	15.9	11.1
Width occipital condyles	27.2	—
Height foramen magnum	6.4	—
Width foramen magnum	7.7	—
Height molar alveoli to lambdoidal crest	41.9	31*
Width glenoid condyles	13.7	—
Length palatonarial border to rostrum tip	56	84
Width palate at P ³	7.3	—
Width palate at M ¹	10	—
Width palate at M ³	8.3	—

The cracked condition of the bone and asymmetry of the left and right lateral wings of the squamosals reveal that the Eppelsheim skull has undergone at least a modicum of postmortem distortion, either during burial or after excavation. Differences between the cast of the ventral side and the specimen itself indicate that some post-excavation restoration has been necessary. Indeed, much of the squamosal region is now plaster of paris. Certain anomalous features of the Eppelsheim skull are discussed later and indicate that restoration has not always been skilful or accurate.

On page 528 Andrews stated 'In *Deinotherium* no development of cellular bone seems to have taken place.' This is clearly wrong. In the Eppelsheim skull, as in the Gebel Zelten skulls, portions of the surface bone are missing to reveal cellular bone beneath. This phenomenon was noted in de Blainville's earlier description of the skull (de Blainville, 1837) and was confirmed by Palmer (1924) in his description of the skull of *P. pentapotamiae*. Skull 6404 : 14 from Gebel Zelten was unfortunately shattered in transit to Bristol but the fragments salvaged leave no doubt that much of the skull was composed of cellular bone.

On page 529 Andrews noted that 'in front of the orbit the maxilla forms a great mass of bone terminating in a rugose, somewhat concave surface for the attachment of muscles'. These concavities are preservation anomalies and not original morphological features. That on the left side is much smaller than the right concavity. In corollary the preorbital swellings of the Eppelsheim skull are unequal, that on the left being much larger. During restoration a large piece of bone has been cemented on to the anterior part of the left swelling thus increasing its total size. This piece of bone is the same length as the concavity on the right side and, if it were to be transferred there, the preorbital swellings would be (a) symmetrical, (b) of similar size and (c) convex.

Further, on page 530, Andrews declared:

'The point of union of the premaxilla (with the maxilla) is probably marked by the sudden narrowing of the snout about 40 cms in front of the orbit.'

This sudden narrowing marks the anterior termination of the preorbital swelling. The 'suture' to which Andrews refers in the next sentence occurs on both the dorsal and ventral surface of the rostrum and bisects both the premaxilla and maxilla. It appears likely that the anterior part of the rostrum was once detached and the 'suture' marks the point of breakage. The actual suture between the premaxilla and maxilla is well seen on Gebel Zelten skull 6404 : 44 and there is no reason to believe that the geometry of these bones differed appreciably on the Eppelsheim skull.

The anterodorsal surface of the external nares appears to be complete and is similar in morphology to the equivalent portion of a skull fragment of *Deinotherium giganteum* from Palencia, Spain. There is no anterior median process in contrast to the condition in Gebel Zelten skull M.26665. The lacrimal bone cannot be observed in the Eppelsheim skull but was more likely to have occupied a similar position to that in 6404 : 44 than to have formed part of the preorbital swelling (cf. Andrews, 1921 : 530), especially as the latter feature is found farther forward

than in the Gebel Zelten skulls. The 'irregularly arranged pits' at the anterior end of the premaxilla (Andrews, 1921 : 531) are not, as Andrews suggested, rudimentary tusk alveoli but dipl e revealed by erosion of the external surface of the bone at this point.

Any comparison made between the occipital regions of the Eppelsheim and Gebel Zelten skulls is liable to be suspect for the roof of the Eppelsheim specimen is incomplete posteriorly. The lambdoidal crest appears to be missing and much of the bone between the foramen magnum and the lambdoidal crest is either absent or distorted (cf. Andrews, 1921 : 527). The shape of the occipital surface of the Eppelsheim skull appears to be more oval than in the Gebel Zelten skulls and the nuchal fossa is shaped differently. The nuchal fossa of the Eppelsheim skull may be divided into two portions—an anterior deep and wide oval pit (long axis transversely orientated) and a posterior triangular trough that is shallower and tapers ventrally. The latter trough may be all that remains of the true nuchal fossa on the Eppelsheim skull.

The 'large post-tympanic flanges' (Andrews, 1921 : 527) are equivalent to the paroccipital processes of other mammals and are, as Andrews described, formed partly of the exoccipitals and partly of the squamosals. The paroccipital processes are smaller in the Gebel Zelten skulls. The 'tongue-like process of bone' (Andrews, 1921 : 527) that is attached to the left paroccipital process was incorrectly identified by Andrews as the paroccipital process itself. This piece of bone is seen only on the left side of the skull and is more likely to represent part of the hyoid bone (cf. Palmer, 1924 : 4). The large convex bulbs that Andrews (1921 : 530; fig. 3) interpreted as tympanic bullae are seen also on Gebel Zelten skull 6404 : 44 where I have interpreted them as bosses for the insertion of the rectus anticus muscles. The tympanic bullae of the Eppelsheim skull are more likely to be represented by a strong crest of bone that terminates posteriorly at the hyoid and extends forward apparently to merge with the pterygoid flange. A petrosal of *D. giganteum* was described by Claudius (1865) but the original specimen is now lost and the accuracy of its identification must be regarded as questionable (pers. comm. H. Tobein).

Munich skull. Stromer (1938) described the remains of a skull, mandible and partial skeleton of *D. giganteum* from the Sarmatian Flinzsande of Munich. Unfortunately all except the cast of the palate were subsequently destroyed and only Stromer's description and diagrams are now available for study. The skull was originally incomplete, lacking the lower part of the occiput, the basicranium, the ventral walls of the temporal fossa and part of the skull roof. However the fragments that were collected are of importance in that they are less distorted than some portions of the Eppelsheim skull.

The rostral flanges of the premaxilla and maxilla are separated in the midline as in the Eppelsheim skull, and are flexed at a similar angle, i.e. less steeply than *Prodeinotherium*. The preorbital swellings were either not developed or have not been preserved. The surface of the skull roof was relatively flat and, as restored by Stromer, may have been more horizontal posteriorly than in the Gebel Zelten skulls. Only the upper portion of the occiput was preserved and was described as

strongly inclined posteriorly, though this cannot be detected from the illustrations given by Stromer. The lateral wing of the squamosal was more vertically aligned than in the Eppelsheim skull and strongly resembles that of *Prodeinotherium*, indicating that the Eppelsheim skull was badly deformed in this region.

Palencia skull. The skull roof and palate of *D. giganteum* from Castrillo de Villavega, Palencia, Spain, is housed in the Madrid Natural History Museum. The nasal bones are represented but are incompletely preserved on the right side. They surmount an external narial opening that is greatly compressed dorsoventrally. The lateral sinuses, which are large on the Gebel Zelten *Prodeinotherium* skulls, are much less prominent in the Palencia specimen. The nasal-frontal suture is fused but the nasals are demarcated as a flat surface projecting anteriorly at an angle from the remainder of the skull roof. The intra-nasal suture is fused and there is no anterior median projection of the nasals over the external nares. The skull roof forms a hollow behind the posterior edge of the nasals and in front of the lambdoidal crest. The lambdoidal crest is incomplete on the right side but on the left extends down the lateral wing of the squamosal to contribute to the widest part of the skull. The postorbital process of the frontal is very large and the anterior portion is located in front of the external nares. Behind the postorbital process the lateral surface of the temporal fossa is strongly delineated from the skull roof, the angle between the two surfaces being in the order of 45° .

Only the dorsal edge of the occipital surface is preserved and this had been incompletely prepared. It is not therefore possible to determine at present whether the occiput was inclined as in the Eppelsheim skull or the Gebel Zelten specimens. The nuchal fossa is incomplete. The shape indicated by the upper part of the fossa is approximately triangular and the dorsal edge of the fossa sited only some 5 cms below the lambdoidal crest. Although the orbit is not represented on this specimen the position of the postorbital processes suggests that the orbit was sited in advance of the external nares in contrast to the situation in the Gebel Zelten specimens.

DISCUSSION. Comparison of the skulls of *Prodeinotherium* and *Deinotherium*, as represented by the Gebel Zelten, Eppelsheim and Palencia specimens, yields evidence of both positive and negative allometric changes. Using the overall skull length as a basis for comparison, parameters that remain the same in both genera are skull width at the external nares, width at the lambdoid crest, and length of the rostrum. The only major increase in width is in the rostral trough of *Deinotherium* and this is exhibited in both the Palencia and Eppelsheim skulls. In both these skulls the external nares are also sited farther posteriorly than in *Prodeinotherium* and are considerably less deep than wide—converging on the elephantoids in both position and shape. The length and width of the skull roof are proportionately smaller in *Deinotherium* than in *Prodeinotherium*. The facial/cranial region ratio remains constant and the decrease in skull roof length in *Deinotherium* is directly proportional to the increase in area of the occipital region due to the anterior inclination of the latter. The shorter skull roof of *Deinotherium* is also correspondingly narrower. This is a compensatory feature to permit a large area of origin of the temporal muscles despite a shorter skull roof.

The majority of the differences between the cranial morphology of *Deinotherium* and *Prodeinotherium* involve only relatively minor allometric changes and some of these are foreshadowed by the differences between the immature (6404 : 44) and mature (M.26665) *Prodeinotherium* skulls. Thus the rostrum is more steeply downturned in M.26665 than in *Deinotherium* and the rostral flexure of 6404 : 44 is even more pronounced. Decrease in rostrum curvature in *Deinotherium*, together with increase of rostral width and retraction of the external nares, suggests the development of a more powerful and effective proboscis in the later genus. The length measurements of 6404 : 44 and M.26665 are very similar but the skull width parameters are relatively smaller in the immature specimen.

In *Deinotherium* the elevation of the occipital condyles, elongation of the paroccipital processes and increase in inclination of the occiput are associated with functional changes enhancing the downward movement of the head (and thereby the tusks). The greater inclination of the occiput has contributed to a decrease in the length of the skull roof, although this is also affected by the more posterior siting of the external nares. The shorter skull roof limits the potential area of attachment of the temporal muscles but this is compensated for by excavation of the temporal fossa and decreased width of the skull roof. In this way major changes in cranial morphology in the Deinotheriidae are associated with proboscis development and with increase in potential movement of the skull on the neck, both factors suggesting changes in feeding methods and habits.

TABLE 4

Deinotherium skull measurements

Parameter	Eppelsheim	Munich	Palencia
Total skull length	109	—	—
Width anterior tip rostrum	34·7	—	—
Length rostrum to external nares	53·5	—	—
Width skull at external nares	79	—	69
Width rostral trough at external nares	49·8	—	32*
Length external nares to lambdoidal crest	29	33	34
Minimum width skull roof	48	40	45
Width at lambdoidal crest	98	—	—
Height lambdoidal crest to foramen magnum	47·3	—	—
Height lambdoidal crest to nuchal fossa	9·4	—	—
Height nuchal fossa	19·5	—	—
Width nuchal fossa	19	—	—
Width occipital condyles	30·5	—	—
Height foramen magnum	5·6	—	—
Width foramen magnum	14·1	—	—
Height lambdoidal crest to molar alveoli	50*	—	—
Width glenoid condyles	27	21	—
Length palatonarial border to rostrum tip	68	—	—
Width palate at P ³	15·8	7·7	—
Width palate at M ¹	18·7	—	—
Width palate at M ³	15	10	—

Mandible

(Plates 4-5)

MATERIAL REFERRED. 6404 : 13, incomplete horizontal rami with tusk fragments and cheek teeth; 6404 : 45, fragmented immature mandible with tusks and dentition; 6412 : 10, tuskless mandible with worn cheek teeth; B.M.(N.H.)M.26666, mandible with tusks and cheek teeth; 6419 : 16, symphysis fragment with tusk alveoli.

DESCRIPTION. Four nearly complete mandibles and a number of mandibular fragments have been collected from various sites at Gebel Zelten. None of the specimens is complete but sufficient information can be derived from the specimens to provide the following composite description.

The horizontal ramus is sigmoid, rising gently in front of M_3 and flexing ventrally at M_1 until at the tusk alveolus it subtends an angle of 115° to the alveolar border. The cheek teeth are erupted in almost parallel rows on the median dorsal surface of the horizontal ramus. The alveolar border is produced anteriorly to form a strong ridge extending from the third premolar to the tusk alveolus. These ridges converge anteriorly and enclose a gutter-like suprasymphysial depression similar to that of the elephantoids. The symphysis itself is broad and extends anteriorly from the vicinity of the posterior root of the third premolar. In one specimen (6412 : 10) a wide and shallow pit is preserved on the ventral and medial side of the horizontal ramus beneath the posterior root of P_3 . The pit may represent the point of insertion of the anterior belly of the digastric muscle. On each ramus there are three mental foramina. In mandible 6404 : 13 the posterior foramen is slightly anterior to the front root of P_3 ; in 6412 : 10 it is level with the hind root of this tooth. In both specimens the anterior mental foramen is sited about 8 cms in front of the posterior mental foramen, and the intermediate foramen varies in location between the two.

Beneath the third premolar the horizontal ramus is oval in transverse section, being deeper than wide and slightly more convex laterally than medially. Beneath M_3 the horizontal ramus has flat and parallel lateral and medial sides and develops a small keel on the ventral surface. The dorsal surface of the horizontal ramus increases in width posteriorly and the lateral surface becomes the leading edge of the ascending ramus when level with M_3 , from which it is separated by a wide, oval and concave platform.

The leading edge of the ascending ramus is nearly at right angles to the horizontal ramus. The coronoid process is small and directed anteriorly. The mandibular condyle is elevated only a short distance above the coronoid process and is a little wider than the latter is long. The condyle is almost cylindrical. The inferior and posterior borders of the ascending ramus are appreciably thicker than the adjoining bone. There is a pronounced notch beneath the dental foramen on the inferior border of mandible 6412 : 10 that may mark the insertion of the sternomandibular muscle. The medial surface of the ascending ramus is divided unequally by a ridge extending from the base of the mandibular condyle to the alveolar border beneath M_3 . A second ridge descends posteriorly from the anteromedial face of the coronoid process and joins the first beneath the hind edge of the coronoid process. The

triangular area thus enclosed serves for the insertion of the temporal muscle (which also occupies a depressed area of similar size on the lateral face of the ascending ramus). The masseter muscle inserts on the lateral surface of the angle of the jaw. The internal pterygoid muscle inserts similarly on the medial surface of the angle and the external pterygoid muscle inserts above the dental foramen and between the mandibular condyle and coronoid process. The digastric muscle inserts on the ventromedial surface of the mandible beneath and in front of the coronoid process.

COMPARISON WITH OTHER DEINOTHERE MANDIBLES. The degree of curvature and length of the mandibular symphysis varies appreciably with the various deinotheria taxa. The mandibular symphysis of *Deinotherium giganteum* is longer and has a more vertically aligned symphysial region than that of *Prodeinotherium bavaricum*. *D. bozasi* of the African Quaternary has a relatively short mandibular symphysis but this is flexed at right angles and therefore more abruptly than in any other deinotheriid taxon. The symphysis of *D. levius* (here interpreted as synonymous with *D. giganteum*) is intermediate in length and degree of flexure between *D. giganteum* (*sensu stricto*) and *P. bavaricum* (Graf, 1957). Arambourg (1934) believed the apparently more acute flexure of *D. levius* separated this taxon from *D. giganteum*, and Laskarev (1944) deduced that *D. levius* had African rather than European affinities. The mandibular symphysis of *P. hobleyi* from Gebel Zelten is similar to that of *P. bavaricum*.

Sahni & Tripathi (1957) separated the two Asian deinotheriid taxa on the basis of the transverse section of the horizontal ramus level with M_3 . In *D. indicum* the jaw bulges on either side of M_3 , the lateral bulge being more pronounced and giving rise to a flat platform on the lateral side of this tooth and in front of the ascending ramus. In contrast, the jaw of *P. pentapotamiae* has a narrow and elliptical cross section. In this respect *P. hobleyi* from Gebel Zelten is similar to *D. indicum*.

Graf (1957) and Bergounioux & Crouzel (1962a) showed that the mental foramina of the mandible varied greatly in position. Those of *D. giganteum* and *D. bozasi* tended, however, to be sited more anteriorly than those of *P. bavaricum*. The mental foramina of the Gebel Zelten *Prodeinotherium* are also sited farther forward than in the examples of *P. bavaricum* quoted by Graf (1957 : 168).

TABLE 5

Prodeinotherium hobleyi mandible measurements

Left horizontal ramus (6412 : 10)

Total length	63
Height at tusk alveolus	12.7
Height at P_3	13.3
Height at M_1	12.3
Height at M_3	11.1
Width at P_3	7.3
Width at M_1	7.7
Width at M_3	10.7

Left ascending ramus (6412 : 10)

Length	22.6
Height at coronoid process	26
Height at mandibular condyle	29*

Mandibular condyle (6404 : 13)

Length	4.7
Width	10.3

Dentition

(Text-fig. 7; Plates 4-5)

MATERIAL REFERRED. 6401 : 4, right maxilla with P³-M³; 6404 : 13, mandible with tusks and cheek teeth; 6404 : 44, immature skull with cheek teeth; 6404 : 45, fragmented immature mandible with tusks and cheek teeth; 6412 : 10, tuskless mandible with worn cheek teeth; M.26665, adult skull with cheek teeth; M.26666, mandible with tusks and cheek teeth; 6401 : 1, LM³; 6404 : 14, LP³-M² and RP³-4; 6409 : 41, M² fragment; 6410 : 2, RP⁴; 6412 : 39, LM²; 6412 : 40, LM₁; 6412 : 54, LP⁴; 6413 : 18, LM³; 6416 : 120, tusk tip; 6416 : 130, tusk; 6421 : 2, LM²; 6404 : 28, 6405 : 48, 6419 : 17, 6421 : 15, 6423 : 13, 6423 : 45, 6423 : 56, enamel fragments.

DESCRIPTION. Teeth are the most commonly preserved deinotheriid remains and differ sufficiently in size and morphology from other Cenozoic mammals to permit ready identification even on incomplete specimens. The terminology employed in previous descriptions of deinother teeth has varied greatly from author to author. The teeth are basically lophodont, the lophs originating through coalescence of adjacent cusps in a bunodont ancestral stock. Terms used here are based on the standard cusp nomenclature (Osborn, 1907) and those used by Osborn for proboscidean teeth (Osborn, 1942). The terms are here used only to express topographic equivalence with the dental characters of other mammals and have no genetic significance.

Superior dentition. Downturning of the rostral region involved the posterior retreat of the external nares, accompanied by withdrawal of the premaxillae to line the floor of the rostral trough. The incisors, canines and anterior cheek teeth were lost during, if not before, the hindward migration of the premaxillae. All lophs and cingula on the upper teeth are rugose until worn. The lingual edges of the transverse lophs are taller than the labial edges and show more wear. A well developed facet is formed on the anterior surface of each transverse loph and extends for the entire width of the loph. Parallel facets are seen also on the anterior and posterior cingula when the tooth is worn sufficiently for these to occlude with the lower dentition.

The third premolar is equant and possesses two internal cusps and an ectoloph (text-fig. 7A). The protocone is the larger cusp and is separated from the hypocone by a deep but very narrow valley. The protocone extends labially and anteriorly to the base of the ectoloph, thus forming a low, incipient protoloph. The hypocone bears a small mesostyle on its anterolingual face. The hypocone is elongate labially but does not form a metaloph. The strong ectoloph is formed by the coalition of the paracone, metacone, and an intermediate cusp that is taller than either. The

posterior end of the ectoloph is continuous lingually with the posterior cingulum that terminates lingually on the posterolingual face of the hypocone. The median valley is wide and open posteriorly; it is deepest between the labial bases of the protocone and hypocone. The anterior cingulum connects the base of the protocone to that of the ectoloph. There are no lingual or labia cingula.

The fourth premolar is bilophodont and subequant, being longer than broad. The ectoloph is less strong than in the third premolar and the intermediate cusp is reduced to a swelling on the anterior face of the metacone. The transverse lophs are not straight, the protoloph being convex anteriorly and the metaloph convex posteriorly. Both lophs are connected labially with the ectoloph. From the posterior lingual face of the protocone a ridge extends posterolabially to the centre of the median valley and a similar ridge extends down the anterior face of the

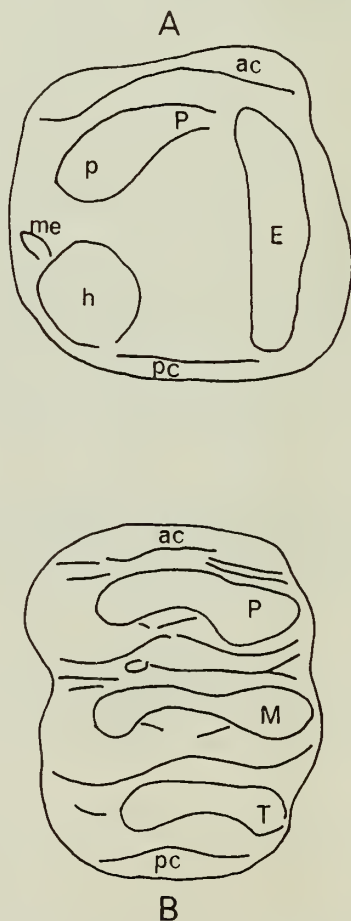


FIG. 7. *Prodeinotherium hobleyi* upper teeth. A = left P³, B = right M¹; Not to scale.

ac = anterior cingulum, h = hypocone, me = mesostyle, p = protocone, T = tritoloph, E = ectoloph, M = metaloph, P = protoloph, pc = posterior cingulum.

hypocone. The metaloph of the fourth premolar is the only loph in the upper dentition to bear a posteriorly directed wear facet. The median valley is widest labially next to the ectoloph and narrows, opening lingually between the protoloph and metaloph. It is almost, but not quite, dammed by a small mesostyle on the anterior face of the hypocone. The anterior and posterior cingula are well developed. There is a minute internal cingulum.

The anterior molar is trilophodont and subrectangular, being longer than wide and narrowest posteriorly (text-fig. 7B). All three lophs bear ridges directed towards the midline of the tooth from their posterolingual and posterolabial edges. The tritoloph (posterior loph) is much less wide than either the protoloph or metaloph and the ridges from the posterolingual and posterolabial edges of the loph are less pronounced than in the protoloph or metaloph. Between the protoloph and metaloph the anterior median valley is blocked labially by a small bune between the paracone and metacone, and lingually by a short spur connecting the protocone to the hypocone. This spur bears a small mesostyle. The posterior median valley, between the metaloph and tritoloph, is much less deep. It is blocked lingually by a short spur connecting the lingual edges of the metaloph and tritoloph, and labially by the junction of sharp ridges extending down the posterior face of the metaloph and anterior face of the tritoloph. The anterior cingulum is strong but the posterior cingulum is less well developed than in the premolars.

The second molar is bilophodont and slightly longer than wide. The protoloph is similar to, but taller than, the metaloph. The centrally directed ridges on the hind face of the protoloph are well developed and stronger than in M¹. The ridge from the lingual edge of the loph extends beyond the midline of the tooth; that from the labial end of the loph is more posteriorly directed and fuses with a similar ridge extending from the crown of the metacone. The median valley is open labially but is bounded lingually by a short spur joining the protoloph to the metaloph. The postmetaloph ornamentation is rather complex. A strong ridge extends from behind the hypocone to join the lingual edge of the posterior cingulum. A more ventrally directed ridge connects that from the hypocone to a posterolabially directed ridge from the metacone, thus forming a subsidiary loph behind the metaloph. The posterior cingulum bears a large style on its labial extremity.

The third molar is subequant, and tapers posteriorly. Like the second molar it is bilophodont. The topography of the protoloph is similar to that of M². The metaloph is less wide than the protoloph, and the postmetaloph ornamentation is simpler. A ridge descends from the hypocone to the lingual termination of the posterior cingulum. The metacone gives off a strongly developed ridge that descends posteriorly and then centrally to the midline of the tooth to connect with the posterior cingulum. In some teeth the metacone ridge is also connected to the hypocone ridge and thus the postmetaloph ornamentation of M³ is more variable than in M². There is no style on the posterior cingulum.

Inferior dentition. Tusks are present in mandibles 6404 : 13, M.26666, and 6404 : 45. The tusks are oval in transverse section with the long axis aligned anteroposteriorly. Enamel was preserved only on the tusks of the immature mandible (6404 : 45) where it covered the entire erupted surface of the tooth. The

tusks in 6404 : 45 are short and nearly straight but in mandible M.26666 they curve downwards until the tip is nearly vertical. The dentine shows no 'engine turning' structure as in *Mastodon* but forms bands parallel to the periphery of the tooth.

As in the superior cheek teeth, all lophi, cingula and isolated cusps of the lower molars and premolars are rugose until worn. Except on P₄, all wear facets on the transverse lophids occur on the posterior surface. The labial edges of the lophids are less high but show more wear than the lingual edges.

The third premolar is triangular and tapers anteriorly. The protoconid is the largest and tallest cusp. It is elongate sagittally and is sited in the midline of the tooth. The protoconid is continued forwards as a high narrow ridge extending to the lingual edge of a very abbreviated anterior cingulum. It is also connected posterolingually to a tall metaconid. From the junction of the protoconid and metaconid, a narrow and less elevated ridge proceeds posteriorly to merge with an elongate hypoconid. This in turn connects with an elongate entoconid via a weakly developed, low, posterior cingulum. A C-shaped hypoconulid may or may not connect with the posterolabial edge of the entoconid. The protoconid and outer face of the ectolophid became worn more rapidly than the remainder of the tooth.

The fourth premolar is bilophodont and represents a wider and more elongate version of P₃. The protoconid and metaconid are set farther apart and are connected by a protolophid that is curved with the convex face posteriorly. The anterolingual extension of the protoconid extends more laterally than in P₃. The protoconid is also joined to the hypoconid by a low ectolophid. There is no hypoconulid but the hypoconid is connected to the entoconid by a hypolophid that is straighter and less tall than the protolophid. There are no well defined wear facets on the hypolophid but the lateral extremities become worn faster than the central portion and small wear facets occur on both sides of the lophid. The hypoconid is connected by a short spur to the strong posterior cingulum.

The first molar is trilophodont, the protolophid and hypolophid being wider than the tritolophid. A strong anterolingual ridge on the anterior face of the labial edge of the protolophid projects towards, but does not join, a weaker anterolabial ridge from the lingual extremity of the lophid. Similar but less strongly developed ridges may be traced on the anterior faces of the hypolophid and tritolophid. The anterior and posterior median valleys are open at both sides. The anterior cingulum is less well developed than the short, centrally placed posterior cingulum that stands proud at the rear of the tooth.

The second and third molars are bilophodont and are differentiated only by the posterior taper on the M₃ and the better developed posterior cingulum on that tooth. From the labial edge of the protolophid a strong medial ridge extends postero-ventrally to meet the anterior cingulum. A similar but less strong ridge extends from the lingual extremity of the lophid. These ridges are duplicated in a less pronounced fashion on the anterior face of the hypolophid. The median valley is open at both ends. As in M₁, the wear facets on the lophids face posteriorly. The posterior cingulum of M₃ is less wide than that of M₂ but is taller, more curved, and extends farther posteriorly.

TABLE 6

Prodeinotherium hobleyi tooth measurements (in mm.)

		Upper premolars							
		6401:	6404:	6404:	6412:	M.26665(l)	M.26665(r)		
		4	14(l)	14(r)	55				
P ³	ap	47.5	56.4	55.3+	—	46.5	43.7		
	prot	—	55.0	—	51.1	—	—		
	met	50.1	55.6	—	—	47.5	46.1		
P ⁴	ap	—	47.1	—	—	47.9	44.9		
	prot	—	62.7	64.0	—	58.5	58.4		
	met	—	60.3	—	—	56.7	57.6		
		Upper molars							
		6401:	6401:	6404:	6413:	M.26665(l)	M.26665(r)		
		1	4	14(l)	18				
M ¹	ap	—	68.6	76.6	—	70.5	71.5		
	prot	—	58.8	60.7	—	62.5	62.9		
	met	—	56.7	60.6	—	61.5	60.2		
M ²	trit	—	47.7	49.2	—	—	50.2		
	ap	—	67.8	73.2	—	70.6	73.1		
	prot	—	67.9	69.0+	—	—	72.7		
M ³	met	—	66.5	64.0+	—	—	76.7		
	ap	75.7	67.2	—	59.3	72.8+	—		
	prot	77.2	67.9	—	62.0	77.6	—		
	met	66.9	62.6	—	—	73.9	—		
		Lower premolars							
		6404:	6404:	6404:	6404:	6410:	6412:	6412:	
		13(l)	13(r)	45(l)	45(r)	2	10(l)	10(r)	
P ₃	ap	43.3	45.5	49.1	50.7	—	39.6	39.7	
	tr	32.3	35.0	40.7	39.6	—	31.7	32.3	
P ₄	ap	54.4	53.1	—	58.9	—	44.3	44.7	
	prot	43.0	43.9	—	46.9	38.4	38.6	39.4	
	hyp	45.6	43.2	—	43.3	34.9	—	—	
		Lower molars							
		6404:	6404:	6404:	6404:	6412:	6412:	6412:	
		13(l)	13(r)	45(l)	45(r)	10(l)	10(r)	39	40
M ₁	ap	70.0	65.3	82.7*	—	55.0	55.3	—	55.1
	prot	48.8	47.0	47.4*	—	38.8	41.8	—	41.1
	hyp	51.0	49.1	48.2*	—	39.5	39.8	—	43.4
	trit	45.9	44.3	38.3	—	33.8	34.2	—	37.6
M ₂	ap	—	71.9	—	76.3	57.0	54.8	—	—
	prot	65.5	61.6	—	61.1	50.3	50.4	52.8	—
	hyp	—	59.0	—	62.2	48.0	49.5	—	—
M ₃	ap	—	—	—	84.0	66.9	67.8	—	—
	prot	—	—	—	63.4	54.1	54.9	—	—
	hyp	—	—	—	59.3	47.6	46.4	—	—

ap = greatest sagittal length;

prot = width at protoloph(id);

trit = width at tritoloph(id);

* = approximate measurement.

tr = transverse width;

met = width at metaloph(id);

hyp = width at hypolophid;

TOOTH FUNCTION IN DEINOTHERES. The function of deinotheres tusks has yet to be satisfactorily explained. Conventional interpretations include pulling branches down to mouth level and digging for food. It is unlikely that deinotheres tusks were used for digging for the following reasons. The tusks would fail to reach the ground unless the animal was either kneeling or standing at a lower elevation than the surface at which digging occurred. Such wear facets as have been observed are not consistent with a digging function. Food excavated from below ground surface would inevitably be contaminated with soil which would result in rapid attrition of the cheek teeth; no compensatory increase in hypsodonty of the deinotheres cheek teeth has been observed.

The tusks of immature deinotheres are covered by enamel. Enamel production apparently ceases shortly after the eruption of the tusks. The absence of enamel on the tusks of mature deinotheres suggests that the enamel-bearing portion was subsequently removed by wear. I have observed wear facets in two places on deinotheres tusks—on the posterior surface of the tusk tip (*P. hobleyi*) and on the anteromedial surface of the tusk tip (*P. hobleyi*, *P. bavaricum*, *D. bozasi*). The anteromedial facets may be attributed to constant abrasion by the proboscis but might conceivably have been produced during the action of stripping bark or branches from vegetation.

A detailed description of the cheek tooth function in deinotheres is in the process of preparation. A summary of the preliminary conclusions is given below. Deinotheres cheek teeth occlude orthally and may be functionally divided into anterior crushing teeth and posterior shearing teeth. In the premolars some shearing is effected during occlusion of the ectoloph and ectolophid. The transverse crests on the premolars serve to prevent anterior dislocation of the jaw during the occlusal stroke of the mandible and perform a crushing function during the recovery stroke. The transverse crests of the deciduous fourth premolars and of the molars have well developed shearing facets—on the anterior surface of the lophs and rear of the lophids. These facets are maintained until the transverse crests have been almost completely removed by wear. In unworn teeth the facets are aligned almost vertically but become progressively more horizontal with wear. The change in angle of the shear facet is seen not only between individuals of different maturity but also within single tooth rows, the facets on the posterior end of the tooth row being oriented more vertically than on the anterior molars.

The anterior crushing battery and posterior shearing battery are reconstituted three times during the life of the individual as follows:

	anterior battery	posterior battery
Juvenile animal	DP2-3	DP4
Immature adult	P3-4	M1
Mature adult	P3-4, M1	M2-3

The anterior trilophodont molar performs different functions at different stages of wear. Initially it serves as a shearing tooth in contrast to the crushing premolars. By the time the second and third molars are fully functioning the anterior molar is often too worn to provide an efficient shearing action and becomes incorporated into the anterior crushing battery.

The width of the anterior molar, its attitude in the alveolus, and its alignment in the tooth row all suggest that it functions primarily as a posterior premolar rather than as an anterior molar. The shearing action of this tooth is of limited duration but sufficient to cope during the transition between deciduous and permanent dentition. The bifunctional nature of the tooth row may well explain why deinotheres failed to develop horizontal tooth replacement as in the elephantoids.

Axial skeleton

(Text-figs 8-13)

MATERIAL REFERRED. M.26667h, left rib head; M.26667i, right neuropophysis of third cervical vertebra; 6419 : 15, atlas vertebra; 6424 : 79, axis vertebra.

DESCRIPTION. *Atlas vertebra*. The atlas vertebra of *Prodeinotherium hobleyi* (text-fig. 8, 6419 : 15) is smaller than that of *Mastodon angustidens* (6412 : 185) from Gebel Zelten. Although the transverse processes of the mastodont atlas are incomplete the *Prodeinotherium* atlas was probably wider. The facets for articulation with the occipital condyles are comma-shaped in both specimens but the mastodont facets are larger, relatively taller, less wide and apparently more concave. Differences on the dorsal edge of the neural arch are especially pronounced. The neural spine of the mastodont atlas forms an elongate transverse ridge with large and widely separated scars for the insertion of the rectus muscles. The *Prodeinotherium* atlas spine is a shorter, blunt protruberance that is bounded by rectus muscle scars that are smaller and face more ventrally than in *Mastodon*. The transverse processes of the mastodont specimens are incomplete but were apparently more horizontal than those of *Prodeinotherium* and are sited higher on the neuropophysis, extending for some 4 cms above the dorsal edge of the axis facet. The odontoid fossa of the mastodont atlas is also incomplete but appears to rise more steeply anteriorly and to be more concave than that of *Prodeinotherium*.

The atlas attributed to *Prodeinotherium* does not articulate well with a *Prodeinotherium* axis vertebra (6424 : 79) from an unknown locality at Gebel Zelten, mainly due to differences in the articular facets. The general proportions of the occluding facets and odontoid fossa and processes are however sufficiently similar for the poor articulation to be attributed to variation between individual specimens.

TABLE 7

Atlas vertebra measurements

Parameter	<i>Prodeinotherium</i> <i>hobleyi</i> 6418:15	<i>Mastodon</i> <i>angustidens</i> M.26656	<i>Loxodonta</i> <i>africana</i> 1961.8.9.82
Maximum length	10.4	10.7 + *	7.8
Maximum height	17.2	20.0	17.9
Width at transverse process	28.7	24.3 +	30.4
Width at occipital facets	18.4	20.7	21.3
Width neural canal	6.1	7.3	8.0
Height neural canal	5.0	5.3	3.9
Width odontoid fossa	5.6	6.5	7.3
Height odontoid fossa	6.2	5.6	6.2
Width at atlas facets	16.7	16.3 *	17.7

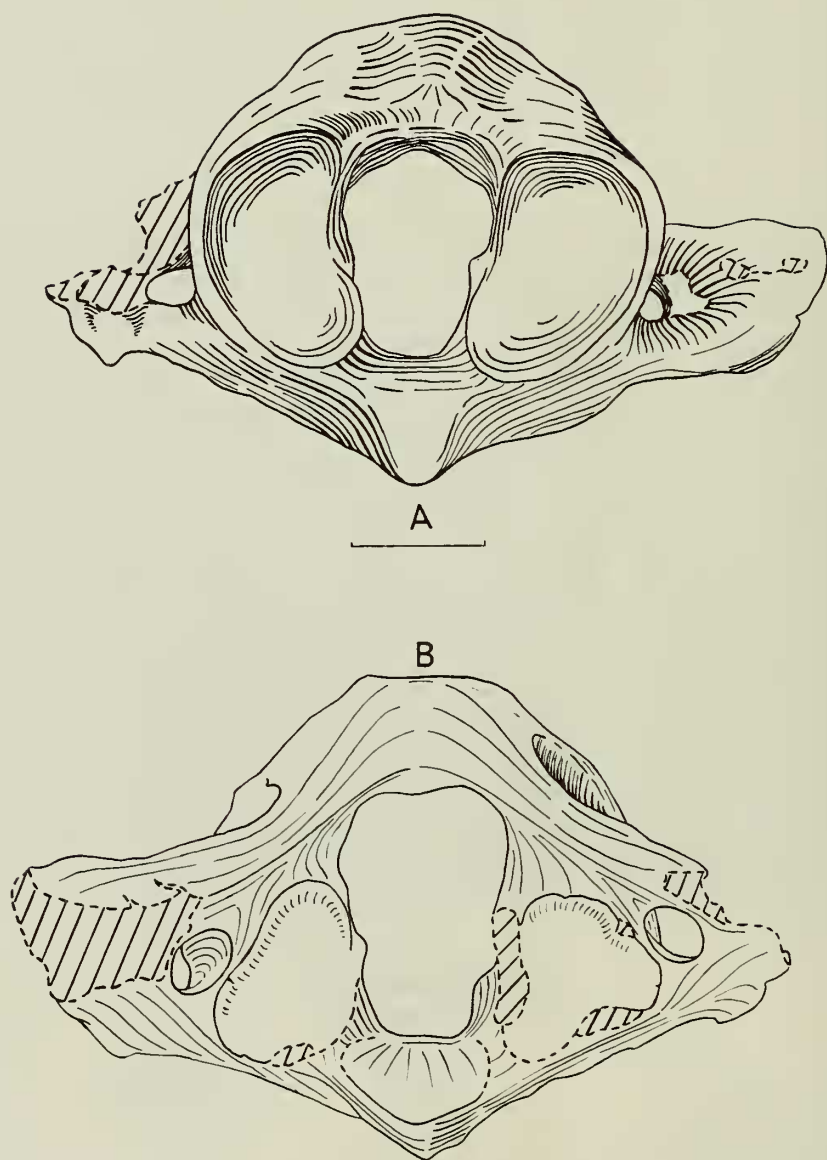


FIG. 8. *Prodeinotherium hobleyi* atlas vertebra.
A = anterior view, B = posterior view. Scale = 5 cm.

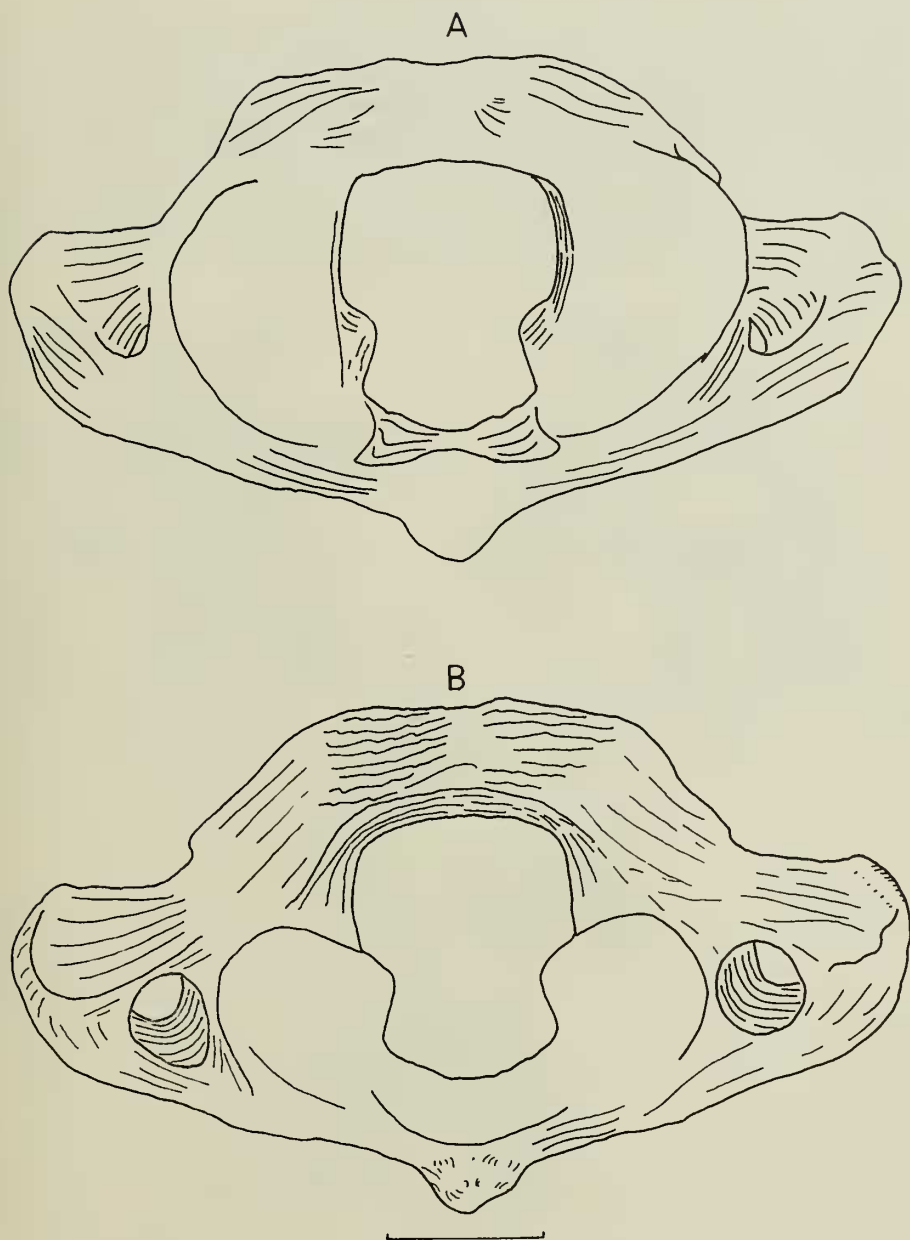


FIG. 9. *Loxodonta africana* atlas vertebra.
A = anterior view, B = posterior view. Scale = 5 cm.

Axis vertebra. The sole deinotheriid axis from Gebel Zelten (6424 : 79) is incomplete dorsally and ventrally (text-fig. 10). In overall size it is slightly smaller than the axis vertebra of the extant African elephant (text-fig. 11) but the odontoid process, although eroded, is longer and stouter in *Prodeinotherium*. The transverse processes are broken at their bases and the entire ventral half of the centrum is missing. The cephalic articular surfaces are oval, extending posteroventrally from above the odontoid process. It is not clear whether, as in *Loxodonta*, the articular facets extend to meet below the odontoid process because they are incomplete. The neural canal is circular in transverse section. The neural arch is notched anteriorly and posteriorly for the passage of the second and third cervical spinal nerves, the posterior notch being the deeper.

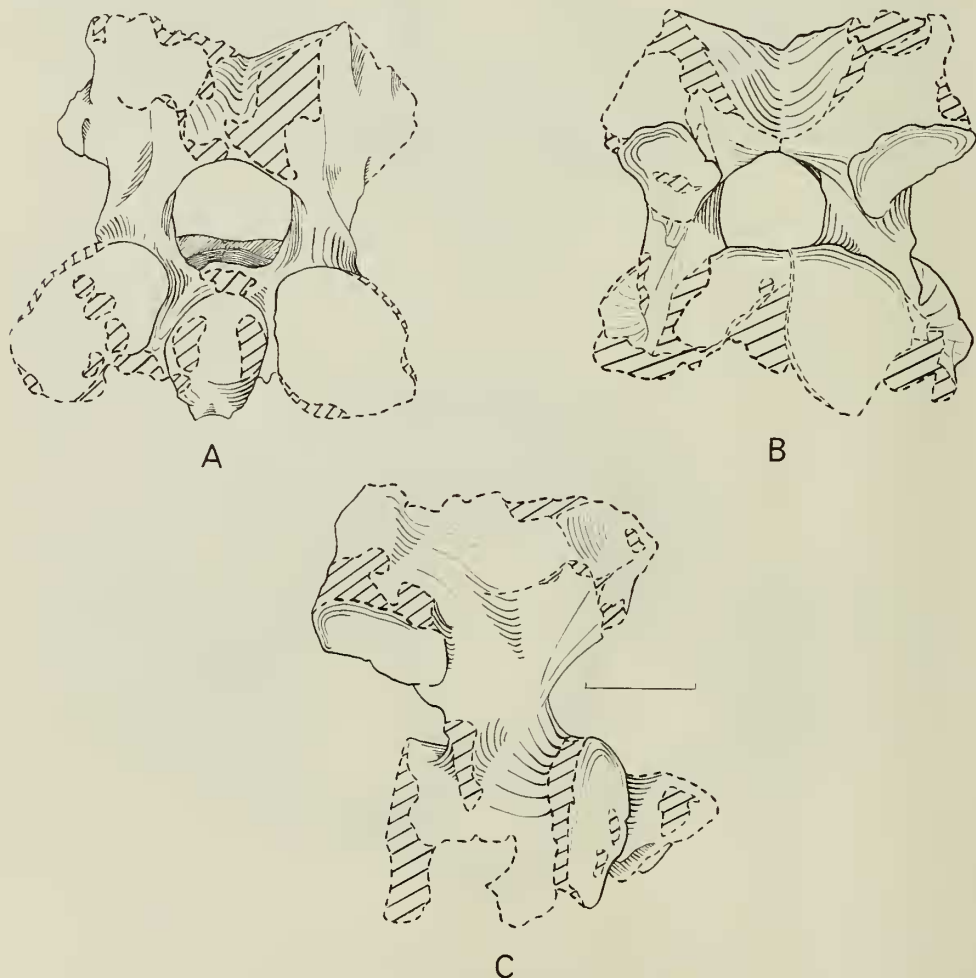


FIG. 10. *Prodeinotherium hobleayi* axis vertebra.

A = anterior view, B = posterior view, C = right lateral view. Scale = 5 cm.

The spine is the most diagnostic feature of the *Prodeinotherium* axis. In the extant elephants 'the neuropophyses blend together above and develop a thick bifurcate spine before coalescing with the centrum' (Owen, 1866 : 547). In the Gebel Zelten axis the neuropophyses are less tall but longer anteroposteriorly than in *Loxodonta*. The bifurcation of the spine is extreme, beginning at the anterior tip of the spine and diverging at an angle of 55° (cf. 30° in *Loxodonta*). The twin crests

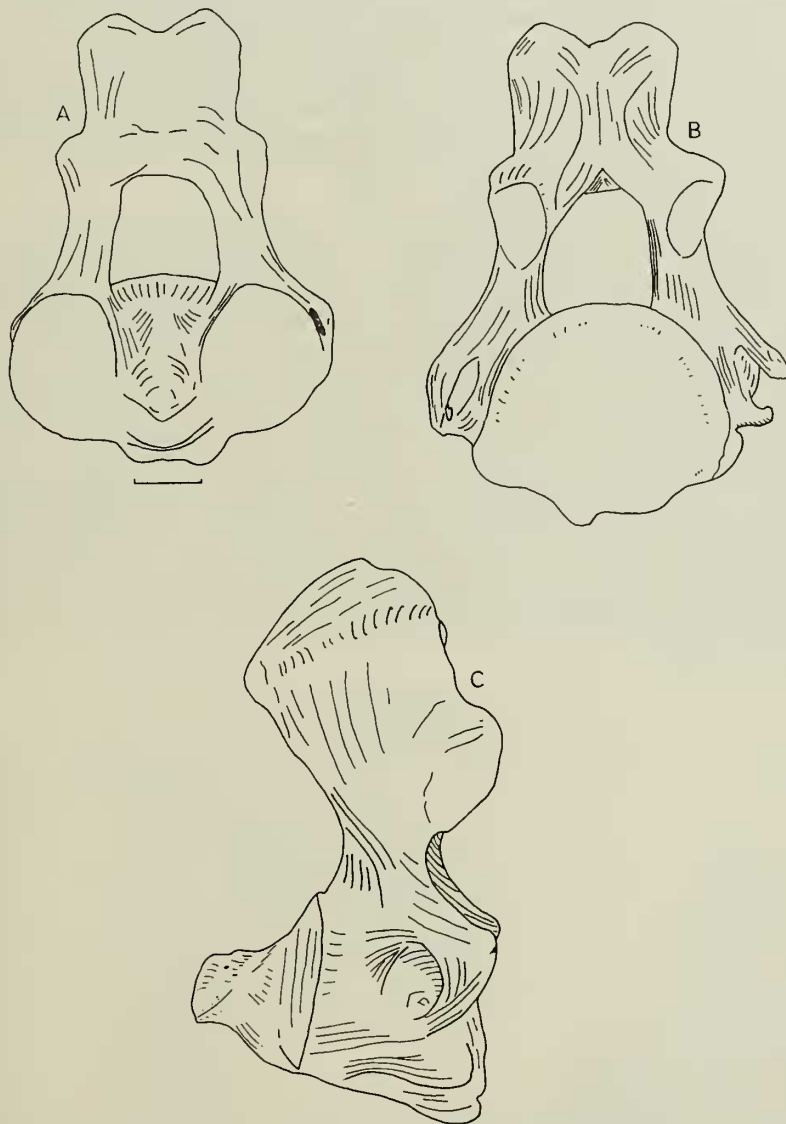


FIG. 11. *Loxodonta africana* axis vertebra.

A = anterior view, B = posterior view, C = left lateral view. Scale = 5 cm.

thus formed ascend backwards less steeply than in the elephant but reach farther posteriorly and are separated by a U-shaped valley that widens posteriorly and descends at an angle of nearly 30° from the horizontal. In *Loxodonta* this valley appears only at the posterior portion of the spine and is horizontal. The post-zygapophyses of the elephant axis are convex; the greater part of the articular surface faces ventrolaterally but the dorsomedial corner faces posteriorly. Much of the articular surfaces of the zygapophyses of the Gebel Zelten *Prodeinotherium* axis are eroded but they are seen to be larger than in the elephant, to be concave and to face ventrolaterally. A small triangular facet may be discerned along the dorsomedial edge of, and at right angles to, the main articular surface but this may have served for the attachment of muscles or ligament rather than for articulation. Above the postzygapophyses much of the bone is missing but this region of the spine must originally have been greatly swollen.

Although the neuropophyses are appreciably wider and longer than those of the elephant, the centrum is only slightly longer. It is not until the relative areas of the neural canals are taken into consideration that the axis of *Prodeinotherium* is seen to be more massive and appreciably longer than that of the African elephant. The larger surface of the neural spine affords a greater area of attachment for the *rectus capitis posterior major* muscle, *obliquus capitis inferior* muscle, *semispinalis capitis* and *semispinalis cervicis* muscles. All four muscles serve to extend the head on the neck or, acting unilaterally, to rotate or flex the head on the neck. The narrow width of each diverging supraspinous crest suggests that the nuchal ligament was inserted only on the posterior portion of the dorsal surface of the supraspinous crest. The great width of the spine reflects the great width of the nuchal ligament that is in turn reflected by the wider fossae for the nuchal ligament on the occiput of *Prodeinotherium* than in elephantoids. The relatively low dorsoventral height of the spine may reflect the elevated condition of the occipital condyles and/or the less elevated head of deinotheres.

TABLE 8

Axis vertebra measurements

Parameter	<i>Prodeinotherium hobleyi</i> 6424.79	<i>Loxodonta africana</i> 1961.8.9.82
Maximum length	17.1	13.4
Maximum width	17.5+	17.5
Maximum height	17.7+	24.6
Width at atlas facets	17.6+	17.2
Width neural canal	5.2	6.2
Height neural canal	5.0	5.8
Width odontoid process	3.9+	3.4
Height odontoid process	4.7	3.6
Maximum length neuropophysis	15.2	11.9
Minimum length neuropophysis	5.5	3.6
Minimum width neuropophysis	15.3	11.7
Height neuropophysis above neural canal	7.6+	8.1
Length postzygapophysis	5.2+	5.5
Width postzygapophysis	5.2+	3.7

Third cervical vertebra. An incomplete right neuropophysis of a third cervical vertebra M.26667i was associated with immature *Prodeinotherium* skeletal elements from Gebel Zelten site D. The specimen (text-fig. 12) is not well preserved but incorporates the region between the neural spine and the vertebral arterial canal. The neural spine is very low and could have been elevated only slightly above the valley separating the two wings of the axis spine. The neural canal is compressed dorsoventrally. The neural arch is longer anteroposteriorly but less stout than in *Loxodonta*. The prezygapophysis is convex and faces anterolaterally. The postzygapophysis is concave and faces ventrally. Both zygapophyses are aligned more horizontally than in *Loxodonta*. The neural arch is notched anteriorly and posteriorly for the passage of the spinal nerves, the posterior notch being deeper and extending

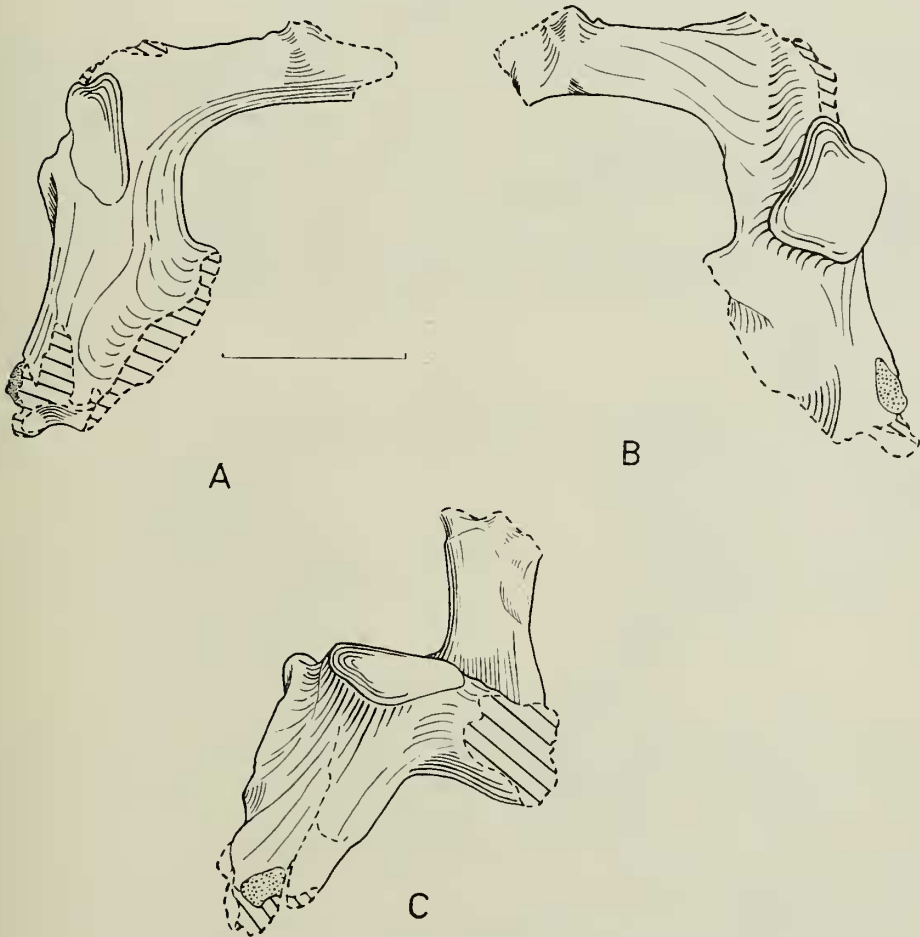


FIG. 12. *Prodeinotherium hobleyi* third cervical vertebra.

A = anterior view, B = posterior view, C = lateral view. Scale = 5 cm.

to the dorsal edge of the vertebral canal. The surface of the bone is not well preserved and muscle attachment areas cannot be detected.

It is interesting that the articular surfaces of the zygapophyses have reversed curvature when compared to the elephantoids in which the postzygapophysis and not the prezygapophysis is convex. This is believed to have some bearing on the direction of movement of the neck in elephantoids as opposed to deinotheres. The centra of the cervical vertebrae of the Gebel Zelten deinotheres shows some flattening anteroposteriorly as in the elephantoids but the neuropophyses are considerably more massive. Taking into consideration the diameter of the neural canal, the cervical vertebrae of the Gebel Zelten *Prodeinotherium* were more elongate than those of *Loxodonta*.

TABLE 9
Measurements of *third cervical vertebra*

Parameter	<i>Prodeinotherium</i> <i>hobleyi</i> M.26667i	<i>Loxodonta</i> <i>africana</i> 1961.8.9.82
Maximum length neuropophysis	7.7+	7.1
Length neuropophysis at neural arch	3.1	2.8
Width transverse process above vertebral canal	2.8	1.9
Width neural canal	7.0+	6.8
Height neural canal	4.4	5.7
Height neural arch above centrum	5.9	9.0

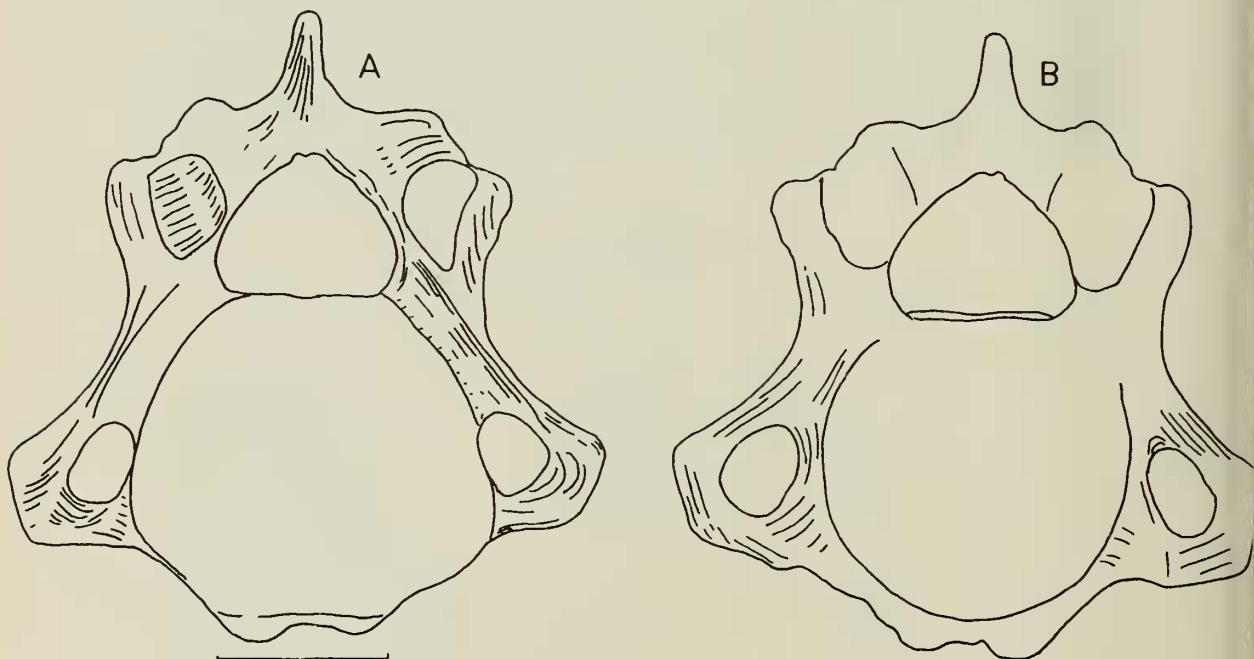


FIG. 13. *Loxodonta africana* third cervical vertebra.
A = anterior view, B = posterior view. Scale = 5 cm.

Rib One left rib was collected with the immature *Prodeinotherium* skeleton from site D. Other rib fragments were noted but were too incomplete to warrant collection. The head of the rib M.26667h is large, rounded and divided by a deep transverse groove into two convex oval facets for articulation with two thoracic vertebrae. The transverse groove is widest medially, and the cranial articulation facet is larger than the caudal. The neck is short and a little wider than the head. On the dorsal edge of the neck is an oval, slightly convex tubercle that articulates above the caudal facet of the head. On the caudolateral side of the tubercle is a rounded prominence, one fourth the size of the tubercle, that may have served for attachment of the longissimus dorsi muscle. The shaft of the rib extends ventrolaterally from the neck but flexes downwards at nearly 40° at the angle. The dorsal surface of the angle bears an elongate prominence for the attachment of the iliocostal muscle. On the cranial surface of the rib, between the head and the angle, there are two elongate fossae. On the caudal surface a deep groove appears midway between the head and angle near the lateral border of the shaft. A transverse section of the shaft proximal to the angle resembles the shape of an hourglass; distal to the angle it is concavoconvex (concave caudally). Distal to the caudal depression the cranial face turns laterally and the transverse section becomes oval and progressively flattened towards the end of the rib. Extending over the cranial surface of the shaft from the angle are a number of irregular prominences that serve for the attachment of various parts of the serratus posticus muscles.

The bicipital head of the rib suggests that it was articulated towards the front of the rib cage.

TABLE 10

Measurement of *Prodeinotherium* rib M.26667h

Parameter	Dimension
Length head	5.3
Width head	5.0
Width neck	5.2
Length neck	3.7
Length neck to angle	10.7
Length at angle	6.8
Breadth at angle	2.7

DISCUSSION. In mammals generally, only one muscle is attached to the anterior face of the arch of the atlas vertebra. This muscle, variously recorded as the *rectus capitis dorsalis minor* (Sisson & Grossman, 1947), *rectus posterior minor* (Jayne, 1898), and *rectus capitis lateralis posterior minor* (Shindo & Mori, 1957) inserts on the occiput lateral to the nuchal fossa and serves to extend the head on the neck. The reduced width of the neural spine of the deinotheres atlas compared to that of elephantoids is due, at least partly, to the fact that the sites of origin of the rectus muscles are closer together and face upwards and outwards rather than forwards. The line of action of the muscles is thus less horizontal and more vertically aligned than in *Mastodon* or the elephants. The change in line of action of the musculature

reflects the different geometry of the occiput of *Prodeinotherium* which has a more dorsally placed nuchal fossa than has that of the elephantoids. The more posteriorly inclined transverse processes may be partly due to a more vertical alignment of the muscles extending from the transverse process to the occiput, or may reflect the importance of muscles originating from the ventral surface of the transverse process to insert on the basicranium and paroccipital process.

The Gebel Zelten *Prodeinotherium* axis differs in many features from that of the elephantoids, the more striking differences being associated with the development of the neuropophyses. The muscles attaching thereto serve to move both the neck on the thorax and the head on the neck. The cross sectional area of the anterior opening of the neural canal of the axis vertebra of *Loxodonta* (ca. 4000 mm²) is half as large again as that of the Gebel Zelten deinotheres axis (ca. 2600 mm²) and if this area may be taken to suggest the relative size of these two mammals (cf. Radinsky, 1967) then the Gebel Zelten deinotheres, although smaller than the African elephant, has much larger and longer neuropophyses than the living animal. It is obvious therefore that the axis of *Prodeinotherium* plays a more important role in the movement of the head and neck than that of *Loxodonta*.

Five major muscles are attached to the axis spine. The *rectus capitis posterior major*, *obliquus capitis inferior*, and *semispinalis capitalis* originate on the axis and move the head about the atlantooccipital joint; the *scalenus* and *semispinalis cervicis* insert on the axis and move the head on the thorax. The lamellar portion of the nuchal ligament also inserts on the spine of the axis. Three muscles possess considerably larger attachment areas on the spine of the *Prodeinotherium* axis than on that of the elephant. These are the *obliquus capitis inferior*, the *rectus capitis posterior minor* and the *semispinalis cervicis*. The former rotates, extends and fixes the atlantooccipital joint (and thereby the head), while the *rectus capitis* extends the head and the *semispinalis cervicis* extends the neck. All three are attached to the upper part of the neuropophysis. That the spine is less elevated than in *Loxodonta* suggests that its function as a lever for moving the head on the thorax is less important than its capacity to move the head on the neck. The external walls of the spine are orientated more laterally than in *Loxodonta* thus affording a more nearly perpendicular line of action for the muscles moving the head and thereby enhancing the mechanical efficiency of these muscles. The sagittal length and divergent nature of the neural spine of the axis also affords a greater area of attachment for the digitation of the lamellar portion of the nuchal ligament.

The postzygapophyses of the axis and zygapophyses of the succeeding cervical vertebrae of deinotheres are more horizontally aligned than in the elephantoids. The curvature differs also—the postzygapophyses of deinotheres are concave and the prezygapophyses convex in direct contrast to the condition normally found in the elephantoids. Thus while the zygapophyses of the anterior cervical vertebrae of elephantoids permit an upward flexure of the neck, those of *Deinotherium* and *Prodeinotherium* flex in the opposite direction. The differences in direction of flexure may be related to the different ways in which the tusks function in deinotheres and elephantoids.

The centrum of the axis is slightly longer in *Prodeinotherium* than in *Loxodonta* and is appreciably longer when the area of the neural canal is used as a basis for comparison. The neural arch of the third cervical vertebra from Gebel Zelten is also longer than its equivalent in *Loxodonta* and it is probable also that this was true of the remaining vertebrae of the neck. Increase in the length of the neck amounts to a decrease in the lever arm of the musculature supporting the head on the neck and moving the head on the thorax. The decrease in lever arm of these muscles reduces their mechanical efficiency, and a larger and stronger musculature is therefore required to support the head on the neck. This is reflected by the large area of insertion of the *semispinalis cervicis* muscles in *Prodeinotherium*. Without access to the cervical vertebrae of *Deinotherium* one cannot deduce whether the relatively long neck of the Gebel Zelten deinotheres is a primitive feature, the neck becoming shorter and mechanically more efficient in later forms, or whether it was a functional adaptation to permit the head to be nearer the ground and thereby enhancing the potential use of the tusks for feeding.

The thoracic vertebrae of *Deinotherium* are incompletely known, the anterior thoracics being best known from the skeleton of *D. 'gigantissimum'* (= *D. giganteum*) from the Pliocene of Manzati, Rumania. The neural spines of these vertebrae are inclined steeply posteriorly. Slijper (1946) pointed out that the neural spines act as levers to transmit muscular force to the centra. The force applied determines the height and direction of the spines. Increase in total body size is accompanied by a relative increase in muscle strength, the size and shape of the spines being therefore dependent also on body size, weight of the head, and length of the neck. The most favourable direction of the neural spine is perpendicular to the muscular force acting on the spine, but intermediate directions are achieved when two or more forces act in different directions upon one spine. In the elephant three main forces are applied to the neural spine of the anterior thoracic vertebrae by the nuchal ligament, the *spinalis dorsi*, and the *multifidus spinae* muscles. Tension in the nuchal ligament exerts a force pulling the spines anteriorly whilst contraction of the muscles pulls the spines posteroventrally.

The funicular portion of the nuchal ligament exerts most of its force on the anterior thoracic vertebrae. The anterior thoracic neural spines of *Loxodonta* are more perpendicular to the centra than those of *Elephas*, although in both animals the spines slope backwards. This indicates that the nuchal ligament of *Loxodonta* is more horizontally aligned and, conversely, that the head of *Elephas* is more elevated with regard to the anterior thoracic vertebrae. Because the nuchal ligament functions most effectively when the lever arm (neural spine) is perpendicular to the line of action of the ligament one may deduce that mammals whose heads are sited above the withers will have backward pointing spines whereas those mammals whose skulls are on the same horizontal plane as the withers will have upright spines. The few mammals with skulls held below the level of the withers will also have vertical neural spines but because the line of action of the ligament will not be perpendicular to the spines the lever arm of the ligament must increase to compensate for reduction in efficiency. The neural spines of these mammals will therefore be

correspondingly longer than those of mammals in which the skull and shoulders are level.

The vertebral column of *D. 'gigantissimum'* was restored and mounted by de Pauw (Stefanescu, 1907; Pl. 1). The neural spines of thoracic vertebrae 2-5 are far more steeply inclined than in those of either of the extant elephants. The original specimens from Manzati, Rumania, were incomplete and their exact length cannot be determined. Backward inclination of these neural spines may be interpreted in two ways: either the head of the deinotheres was carried above the shoulders (the backward inclination being influenced by the line of action of the nuchal ligament) or the vertebral column was rigid (the position of the spines being determined by the multifidus muscles). Total length as well as the angle of inclination of the neural spines must be considered before either alternative can be fully investigated. With regard to the rigidity of the vertebral column, none of the extant graviportal mammals can flex their lumbar and thoracic vertebrae. In view of the large size of the deinotheres it seems likely that the vertebral column would have been similarly modified and perhaps the extreme spinal inclination suggests extreme inflexibility.

Appendicular skeleton

(Text-figs 14-16)

MATERIAL REFERRED. M.26667a, distal end of fibula; M.26667b, right ulna; M.26667c, proximal end of right humerus; M.26667d, right femur; M.26667e, left ulna; M.26667f, scapula; M.26667g, left innominate; M.26667j, proximal and distal end of left radius; M.26667k, distal end of right humerus; M.26667l, distal end of left humerus; 6405 : 98, left cuneiform.

DESCRIPTION. *Scapula*. An almost complete right scapula (M.26667f, text-fig. 14) was associated with the immature skull from Gebel Zelten site D. The left scapula was also present but was partly overlain by skull 6404 : 44 and was destroyed during excavation of the latter. The fragility of scapula M.26667f resulted in the collapse of the vertebral border and cranial and caudal angles during transportation from the site but these portions were subsequently restored with the aid of photographs taken at the site.

The articular fossa is broad and concave. The scapular tuberosity is poorly developed but the coronoid process is well defined. The scapular notch is deeply indented. The spine divides the lateral surface of the scapula into supraspinous and infraspinous fossae of similar proportions to those of *Elephas maximus*. The spine attains its highest elevation in its ventral third at the point of divergence of the acromion and metacromion. From here it descends gradually to the neck and caudal angle. Near the neck the cranial surface of the spine is concave but becomes convex near the cranial angle. The reverse is true of the caudal surface.

Although the scapula is similar in size to that of the Indian elephant, the caudal angle is sited dorsal to the point of divergence of the acromion and metacromion. In the Indian elephant the base of the acromion is level with the caudal angle. The

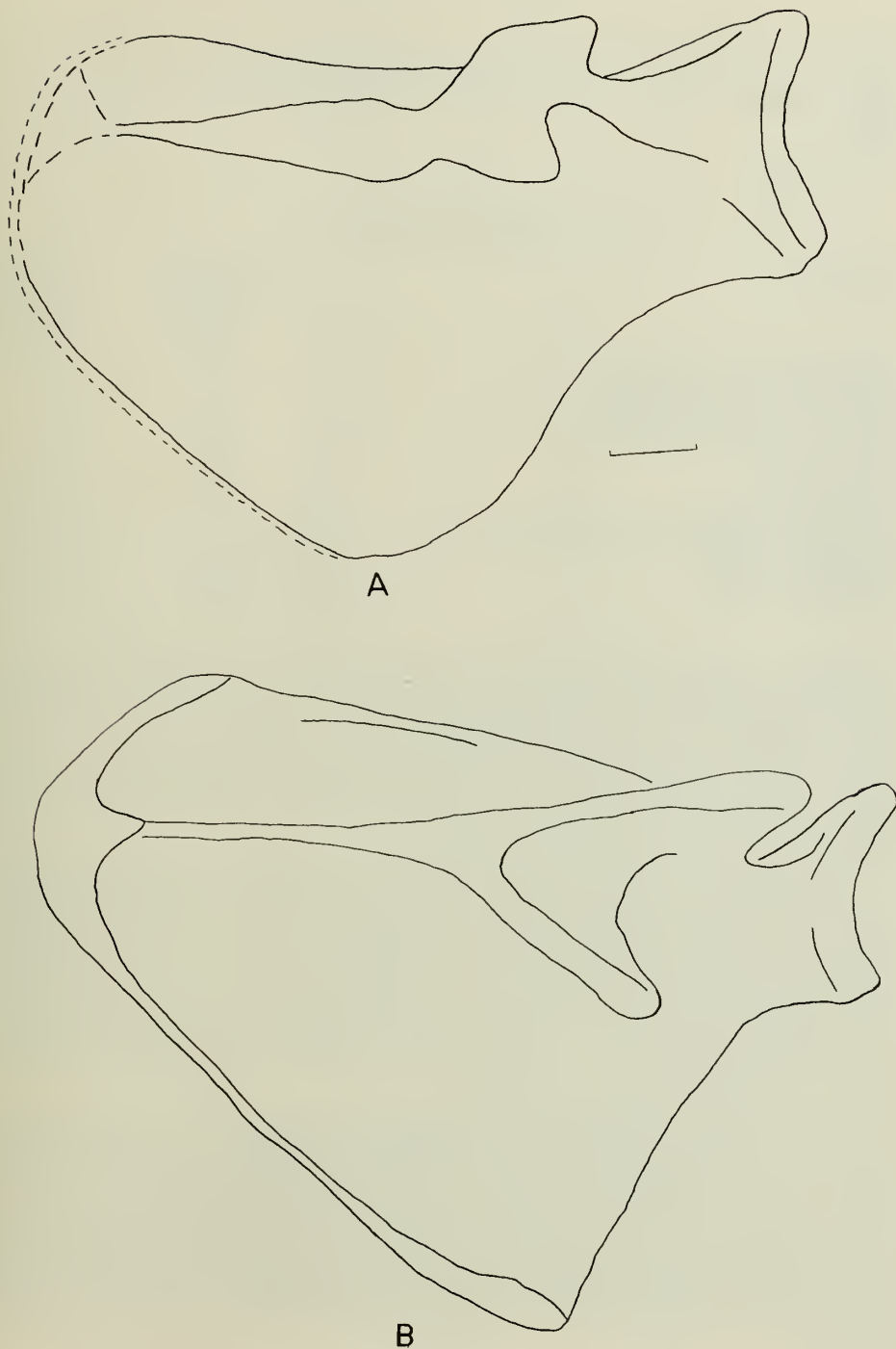


FIG. 14. Right scapula of (A) *Prodeinotherium hobleyi* and (B) *Elephas maximus*. Scale = 5 cm.

head of the *Prodeinotherium* scapula is wider and less concave than that of the elephant and the spine ascends more gently from the neck than in *Elephas*. The scapular notch is deeper and the scapular tuberosity less pronounced than in *Elephas*.

TABLE II

Scapula measurements

Parameter	<i>Prodeinotherium</i> <i>hobleyi</i>	<i>Elephas</i> <i>maximus</i>
	M.26667j	U.B.20189
Length head to vertebral angle	52+	62
Transverse width at caudal angle	35	42
Length caudal angle above head	25	15
Length caudal angle behind spine	26	30
Length spine	40	44
Length acromion	9	17
Length metacromion	6	16
Maximum width spine behind metacromion	5	3.7
Width head (straight)	15.3	14.3
Width head (curved)	17	16
Depth head	10*	8.3

Humerus. The distal extremities of a right and left humerus M.26667k and M.26667l) were associated with the immature skull 6404 : 44. They are complete from the condyles to the deltoid tuberosity and proximal end of the lateral supracondyle ridge. This part of the bone is slightly shorter proximodistally than the equivalent part of the humerus of the Indian elephant but is appreciably wider and deeper suggesting a larger area of origin of the many flexor and extensor muscles that arise from this portion of the humerus.

In cranial aspect the distal end of the musculospiral groove is seen to curve laterally towards the proximal end of the lateral supracondylar ridge. This is a strong ridge, straighter and more salient laterally than its equivalent in the elephant. As in *Elephas* the lateral epicondyle does not project very far laterally but it is stronger cranially in *Prodeinotherium*. Medial to the lateral epicondyle there is a small but deep fossa separated by a low ridge from the very wide but shallow coronoid fossa. The median epicondyle of the trochlea is larger than the lateral, the disparity in size being more pronounced than in *Elephas*.

In caudal aspect the lateral and medial epicondylar ridges are considerably wider than their counterparts in *Elephas*, as are also the epicondyles. Thus, despite the great overall width of the distal portion of this bone, the olecranon fossa is considerably narrower than in *Elephas*. In *Elephas* the epiphysal suture between the median epicondyle and the condyle is aligned diagonally whereas in *Prodeinotherium* it runs medially, thereby increasing the area of the condyle. The anconeal process of the *Prodeinotherium* humerus is narrower but no more salient than that of *Elephas*.

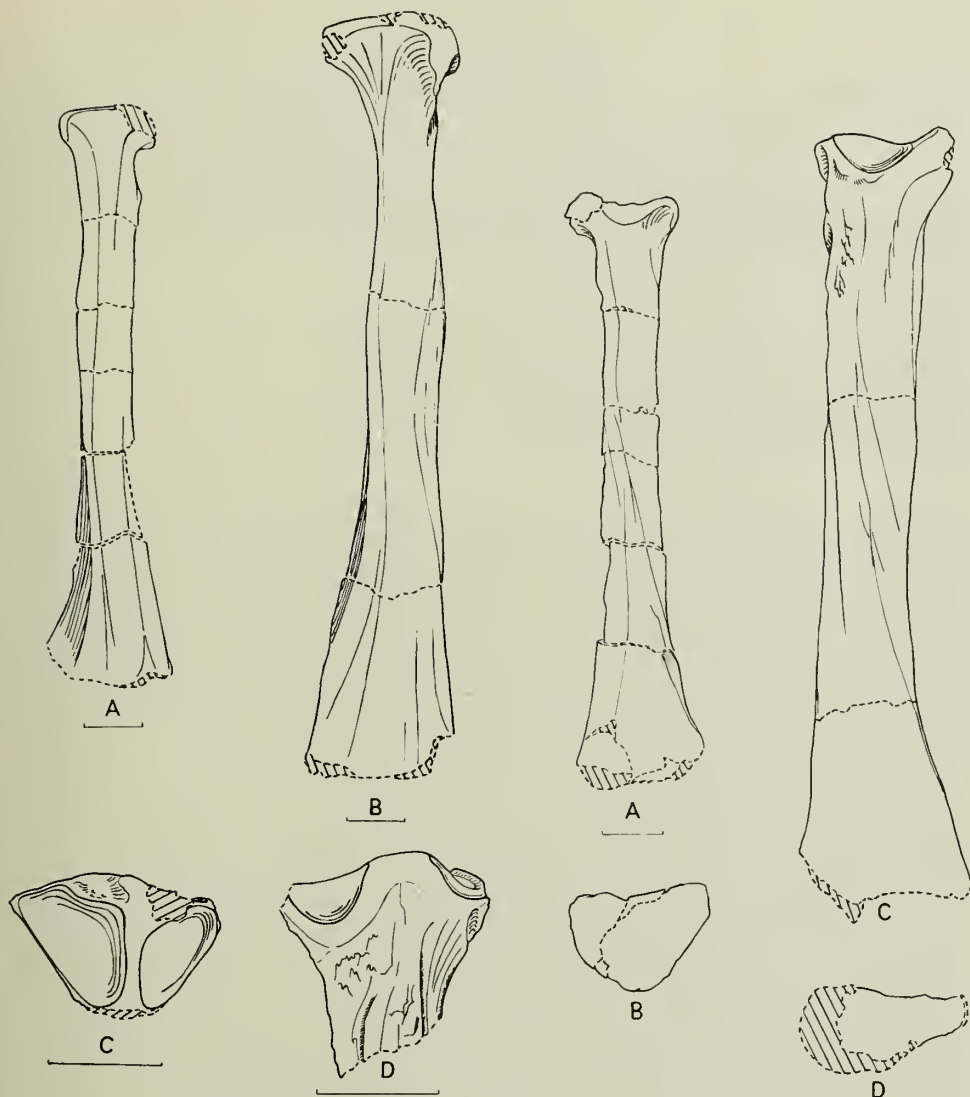


FIG. 15

FIG. 16

FIG. 15. Radius of *Prodeinotherium hobleyi* and *Mastodon angustidens*.

A = *P. hobleyi* left radius (M.15429), cranial view

B = *M. angustidens* right radius (6412 : 166), cranial view

C = *P. hobleyi* head of left radius (6404 : 41), dorsal view

D = *P. hobleyi* head of left radius (6404 : 41), caudal view

FIG. 16. Radius of *Prodeinotherium hobleyi* and *Mastodon angustidens*.

A = *P. hobleyi* left radius (M.15429), caudal view

B = *P. hobleyi* left radius (M.15429), distal view

C = *M. angustidens* right radius (6412 : 166), caudal view

D = *M. angustidens* right radius (6412 : 166), distal view

Scale = 5 cm.

TABLE 12

Humerus measurements

Parameter	<i>Prodeinotherium</i> <i>hobleyi</i>		<i>Elephas</i> <i>maximus</i>
	M.26667k	M.26667l	U.B.20189
Width at dorsal edge of lateral epicondyle	18.5	18.3	14.6
Length from lateral epicondyle to distal end of condyle	19.7	19.7	14.6
Width at median epicondyle	20.5	20.9	19.0
Length from median epicondyle to distal end of median condyle	14.0	13.4	10.5
Width of articular surfaces on condyles	16.2	16.7	15.3
Depth at median epicondyle	14.2	14.8	13.4
Minimum width shaft above lateral epicondyle	9.4	10.1	7.7
Minimum depth shaft above lateral epicondyle	9.2	9.3	7.6
Depth of articular surface of median condyle	12.0	10.2	12.1
Depth of articular surface of lateral condyle	10.2	10.2	11.0

Radius. Only two proboscidean radii have been collected from Gebel Zelten—the head and neck of a left radius of *P. hobleyi* (text-fig. 15C and D; M.26667j) and a nearly complete right radius (M.26654; text-figs 15 and 16) of *Mastodon angustidens*. Two left proboscidean radii from East African Miocene localities are present in the collections of the British Museum (Natural History). That from Rusinga (B.M. (N.H.)M.21872) was attributed to *P. hobleyi* by MacInnes (1942) but belongs to *Mastodon angustidens*. The other specimen (B.M. (N.H.)M.15429) is from Maboko Island and belongs to *Prodeinotherium* (text-figs 15 and 16).

The proximal articular surface of the radius of *Mastodon angustidens* is trapezoidal in outline, with the medial side longer than the lateral. The capitular depression for articulation with the humerus is not large and extends through the centre of the articular surface parallel with the caudal and cranial edges. At right angles and distal to the capitular depression, articulation facets for the ulna occur on the medial and caudal sides, the medial facet being the smaller. Beneath the neck and caudal edge of the median articulation facet for the ulna, the radius is swollen to produce a radial tuberosity for the insertion of the *biceps brachii* muscle. This tuberosity is more pronounced than in *Prodeinotherium* or *Elephas*. Immediately below the radial tuberosity the shaft is approximately rectangular in transverse section, the caudal and cranial edges being the longest and the lateral edge being slightly shorter than the medial. Distally the medial and lateral edges diverge and the shaft is compressed craniocaudally but whereas the shaft of *M. angustidens* retains this shape throughout its length, that of *Prodeinotherium* becomes more equant in its distal half.

Halfway down the shaft of *M. angustidens* the medial edge of the cranial surface is flattened for the insertion of the pronator teres muscle. The interosseous crest extends down the medial side of the caudal face from beneath the radial tuberosity. Distal to the insertion of the *pronator teres*, and at the proximal end of the distal third of the shaft, the interosseous crest diverges, a strong ridge extending towards the medial edge of the epiphysis and a weaker ridge towards the lateral. Lateral

to the interosseous crest is a deep depression extending from the radial tuberosity to the distal fourth of the bone.

The radius of *Prodeinotherium* is smaller than that of *M. angustidens* and is less straight proximodistally and craniocaudally. The radial tuberosity is comparatively less well developed and the interosseous ridge diverges halfway down the shaft. The distal extremity is less wide and deeper craniocaudally than in *M. angustidens*. The radii of both *M. angustidens* and *P. hobleyi* are of similar length to the radius of *Elephas maximus* but the shafts are much wider and the entire bone stouter.

TABLE 13
Radius measurements

Parameter	<i>Prodeinotherium hobleyi</i>		<i>Mastodon angustidens</i>		<i>Elephas maximus</i>
	M.26667j	M.15429	M.26654	M.22872	U.B.20189
Length head to distal epiphysis	—	48	63	59	43
Width proximal epiphysis	5.8	5.0+	7.0	6.5	4.6
Depth proximal epiphysis	9.0+	8.5	10.3	8.5+	8.5
Width at distal epiphysis	—	10.6	13.7	14.5	10.1
Depth at distal epiphysis	—	8.3+	7.9+	6.9	6.5
Width at centre of shaft	—	5.4+	7.5	7.1	4.3
Depth at centre of shaft	—	4.1	3.5	3.7	3.1

Ulna. Right and left ulnae were associated with skull 6404 : 44 but the shaft of the left ulna (M.26667e) is shattered and only the right ulna M.26667b could be prepared completely. The right ulna lacks the distal and olecranon epiphyses and also the proximal portion of the semilunar notch including the anconeal process. The bone is approximately equal in length to that of the extant Indian elephant. The proximal extremity is the stoutest part of the bone and the olecranon, even without the epiphysis, is larger than the olecranon plus epiphysis of the Indian elephant. On the posterolateral side of the semilunar notch is a large scar marking the insertion of the anconeus muscle. A coronoid process projects cranially on either side of the radial notch, the medial process being the larger. The ulnar tuberosity, located on the craniomedial side of the ulna and separated from the medial coronoid process by a large depression, is less well developed for the insertion of the *brachialis* muscle than is the equivalent tuberosity in the elephant.

The middle third of the ulna shaft is triangular in transverse section with cranial, medial and lateral faces but reverts to a pentagonal cross-section at the distal epiphysis. The interosseous ridge extends distally along the medial edge beneath the ulnar tuberosity but dies out at the proximal edge of the distal third of the shaft. Flat surfaces on the caudal aspect of the bone mark the areas of attachment

of the *external pollicis longus*, *extensor communis* and *flexor digitorum profundus* muscles and the ligament humeroantibrachialis. These are all developed much as in the Indian elephant. The shaft is of similar length to that of the Indian elephant but is considerably deeper and wider.

TABLE 14

Ulna measurements

Parameter	<i>Prodeinotherium</i> <i>hobleyi</i>		<i>Elephas</i> <i>maximus</i>
	M.26667b	M.26667e	U.B.20189
Length from olecranon to distal epiphysis	61*	53*	63
Width olecranon	13.6	12.2	15.2
Depth olecranon below semilunar notch	11.7	12.2	13.2
Width semilunar notch	7.6	—	6.7
Width coronoid processes	19.4	—	15.4
Width distal end of shaft	11.8	10.9	12.2
Depth distal end of shaft	13.7	14.7	11.9
Width midpoint of shaft	8.4	—	6.3
Depth midpoint of shaft	7.0	—	6.3

Carpal bones. A small number of carpal bones have been collected from Gebel Zelten sites. MacInnes (1942) reported several carpals from Rusinga Island, Kenya, and these he attributed to *P. hobleyi*. Examination and comparison of the East African and Gebel Zelten material has revealed that only three of MacInnes' specimens may definitely be attributed to *Prodeinotherium*—an incomplete left cuneiform (M.21875), a right magnum (M.21877) and a left unciform (M.21882). These are redescribed with the Gebel Zelten material.

Cuneiform. The left cuneiform from Gebel Zelten (6405 : 98) is better preserved than that from Rusinga. The proximal surface that articulates with the ulna bears two articulation facets (a median rectangular facet and a lateral triangular facet) separated by a sagittal ridge. In *Elephas* and *Mastodon* the proximal articular surface of the cuneiform is saddle-shaped with a transverse depression through the centre. The distal surface of the deinotherium cuneiform bears a triangular concavo-convex facet for articulation with the unciform, much as in the elephant or mastodon. On the caudal border there is a triangular facet for articulation with the pisiform, the hypotenuse of the triangle being bounded by a deep groove extending down the large posterolateral process from the caudal junction of the proximal facets. The distal surface of the posterolateral process of the Gebel Zelten cuneiform is eroded but, as in *Elephas*, it bears a facet for articulation with the fifth metacarpal. The medial surface bears a cranial and (larger) distal facet for articulation with the lunar.

TABLE 15

Cuneiform measurements

Parameter	<i>P. hobleyi</i> 6405:98	<i>D. giganteum</i> (Höwenegg)	<i>M. angustidens</i> M.21874	<i>E. maximus</i> U.B.20189
Maximum length	8.5	15.6	8.6	7.9*
Maximum width	11.7	19.3	11.0+	11.1
Depth cranial face	4.8	9.3	5.0	4.6
Depth caudal face	5.0	8.1	5.3	5.1*
Length proximal facet	6.3	11.9	5.9	5.5*
Width proximal facet	9.1	14.7	8.4+	7.7
Length distal facet	7.1	14.8	8.2	6.5
Width distal facet	7.5	13.6	8.0	7.5
Length posterolateral process	3.6	7.0	4.0	3.9
Width posterolateral process	5.0	6.3	—	3.5
Depth posterolateral process	7.6	9.5	—	7.1

Lunar. An incomplete lunar (M.21876), identified by MacInnes (1942) as the left lunar of *Prodeinotherium hobleyi* is almost certainly mastodont. However the right lunar of both *P. hobleyi* and *Mastodon angustidens* are present in the collections of the Centre for Prehistory and Palaeontology, Nairobi. The *Prodeinotherium* lunar (KNM-RU 1291) is triangular and almost complete although the lateral edges are somewhat irregularly preserved. The facet articulating with the radius occupies nearly the whole of the proximal surface and extends nearly to the caudal edge of the bone. In contrast, that of *Mastodon* terminates cranially. The radial facet is convex in the anteroexternal corner but concave over the remainder of the cranial surface. The ulnar facet at the anteroexternal corner is rhomboid and not triangular as in *Mastodon*. The magnum facet on the distal surface is convex cranially and concave caudally.

TABLE 16

Lunar measurements

Parameter	<i>P. hobleyi</i> KNM-RU1291	<i>D. giganteum</i> (Höwenegg)	<i>M. angustidens</i> KNM-RU 1260	<i>E. maximus</i> U.B. 20189
Maximum length	8.7	16.0	10.3	8.1
Maximum width	8.7	15.4	10.8	8.1
Maximum depth	5.8	10.8	7.1	5.3
Length radial facet	7.3	11.4	7.5	6.7
Width radial facet	7.3	13.6	8.5	6.0
Length magnum facet	7.7	13.9	9.0	7.1
Width magnum facet	8.0	13.4	8.6	7.2
Length ulnar facet	4.2	7.0	5.4	3.2
Width ulnar facet	3.5	4.3	4.0	2.9

Magnum. The right *Prodeinotherium* magnum from Rusinga (M.21877) is incompletely preserved but is more complete than a left magnum of *Mastodon angustidens* from Gebel Zelten (M.26652) that provides a basis for comparison. In *Prodeinotherium* the proximal surface of the magnum articulates with the lunar

and is L-shaped, a postero-medial projection (the foot of the L) standing proud. In *Mastodon* or *Elephas* this projection merges gradually with the body and is relatively less distinct. The proximal facet of the deinothere magnum is divided into two portions—an almost flat cranial surface for articulation with the cranial part of the lunar and a convex caudal region that occludes with the caudal part of the lunar and scaphoid. The scaphoid articulates with the caudomedial projection of the magnum. The distal articular facet is pear-shaped (stem posterior) and concave for articulation with the third metacarpal. Four facets may be discerned on the medial side. The cranioproximal, craniodistal and caudoproximal facets are triangular and denote points of contact with the trapezoid. A mediodistal facet extends anteriorly beneath the craniodistal facet to articulate with the second metacarpal. The lateral side of the magnum adjoins the unciform and four facets may be observed. Two large proximal facets are separated by a central groove in contrast to the situation in the elephantoids in which the facets are contiguous. The distal unciform facets on the magnum are also separated, in contrast to the situation in *Elephas*, but the craniodistal facet is poorly developed as in *Mastodon*.

TABLE 17

Parameter	Magnum measurements			
	<i>P. hobleyi</i> M.21877	<i>D. giganteum</i> (Höwenegg)	<i>M. angustidens</i> M.26652	<i>E. maximus</i> U.B.20189
Maximum length	8.5	15.3	11.2	8.7
Width cranial edge	5.7	10.2	6.9	7.1
Width caudal edge	6.8	10.0	6.8	7.1
Depth cranial edge	5.7	10.4	6.7	6.2
Depth caudal edge	7.7	13.4	—	7.8
Length proximal facet	7.8	14.7	9.2	7.6
Width anterior edge				
proximal facet	4.7	9.9	6.6	7.1
Width posterior edge				
proximal facet	6.6	10.0	6.8	7.1
Length distal facet	6.8	14.0	—	6.7
Width distal facet	4.5	6.2	5.3+	4.5

Unciform. Three unciforms of *Mastodon angustidens* M.26653, M.26655, M.26657) are known from Gebel Zelten and contrast strongly in several features with the left *Prodeinotherium* unciform (M.21882); described by MacInnes (1942). In *Prodeinotherium*, the dorsal facet for articulation with the cuneiform is roughly triangular in outline. It reaches its maximum width at the anterior edge and tapers posteriorly. The cranial and caudal portions are convex but are separated by a transverse concave depression. The facet reaches its highest elevation at the caudomedial edge. The medial surface of the *Prodeinotherium* unciform bears a large proximal and two smaller distal facets for articulation with the magnum. Similar facets are also exhibited by *Elephas* and *Mastodon*. Three facets are apparent on the distal surface of the unciform. The medial facet is elongate, faces distomedially, is divided into two by a concave transverse groove and supports the lateral edge of the third metacarpal. The central facet is triangular (tapering posteriorly), is concave and

articulates with the fourth metacarpal. It is separated from a larger rectangular, convex facet for Metacarpal V by a sagittal groove that is deepest posteriorly. Adjacent to the caudolateral edge of the McV facet but extending onto the proximal surface of the bone is a small, triangular, concave facet for the pisiform.

In the Gebel Zelten mastodont unciforms the cuneiform facet approximates to a rhomb and is longer than broad, the maximum breadth being achieved near the rear of the bone. In *Elephas* this facet is appreciably wider than long, the caudal edge being wider than the cranial, although the latter is relatively wider than in *Mastodon*. The distal facets of the Gebel Zelten mastodont unciforms are arranged much as in *Prodeinotherium* but are more elongate anteroposteriorly. These facets are of similar length in *Prodeinotherium* and the Indian elephant but in the latter the facets for McIV and McV are subequal in size and that for McIV is almost flat.

TABLE 18

Unciform measurements

Parameter	<i>P. hobleyi</i> M.21882	<i>D. giganteum</i> (Höwenegg)	<i>M. angustidens</i> M.26655	<i>E. maximus</i> U.B.20189
Maximum length	9.2	16.4	10.6	8.4
Maximum width	10.3	17.5	11.6	9.3
Maximum height	8.9	10.9	8.9	6.6
Length cuneiform facet	7.6	14.8	8.3	6.5
Width cuneiform facet	9.0	16.2	8.5	9.1
Length McV facet	6.8	8.9	6.5	5.9
Width McV facet	4.2	5.3	5.0	3.9
Length McIV facet	6.7	12.2	7.0	5.2
Width McIV facet	4.7	8.7	6.5	5.4
Length McIII facet	5.1	13.1	5.5	5.9
Width McIII facet	1.6	3.6	1.3	2.0

Pelvis. One half of a pelvis (M.26667g) was associated with the immature deinotheres skeleton from Gebel Zelten site D. It may have belonged with the juvenile skull (6404 : 44), the adult skull (6404 : 14) or neither. Unfortunately the pelvis was shattered during transportation from the site.

Femur. A right *Prodeinotherium* femur (M.26667d) was associated with skull 6404 : 44. It lacks both the head and the distal epiphysis but the shaft is approximately the same length as that of the extant Indian elephant. The shaft is compressed craniocaudally and is virtually straight. The greater trochanter was developed much as in *Mastodon* or *Elephas*. The lesser trochanter is poorly preserved. The distal half of the cranial surface of the shaft bears a large ridge that becomes more swollen distally as it extends towards the patellar surface. This ridge is comparatively larger than in *Elephas* and suggests a larger area of attachment for the vastus intermedius muscle. The caudal surface of the *Prodeinotherium* femur, where preserved, strongly resembles that of the Indian elephant.

TABLE 19

Parameter	Femur measurements	
	<i>Prodeinotherium hobleyi</i> M.26667d	<i>Elephas maximus</i> U.B.20189
Length shaft	78.7	80
Width shaft at proximal epiphysis	25.5+	22.9
Depth shaft at proximal epiphysis	12.2+	10.7
Width shaft at distal epiphysis	20.8+	16.4
Depth shaft at distal epiphysis	17.6+	13.0
Width at centre of shaft	11.3	8.6
Depth at centre of shaft	9.6	6.5

Fibula. The distal third of the shaft of a *Prodeinotherium* fibula (M.26667a) was associated with skull 6404 : 44. The anterointernal border or interosseous ridge is separated from the anteroexternal border in the proximal half of the specimen by a narrow and flat anterior surface. The two borders converge in the distal half and the external border fades out before reaching the distal extremity. The posterior surface is round and broad but forms a sharp ridge immediately above the distal extremity. The lateral face is convex outwards and presumably served for the attachment of the *peroneus brevis* muscle. The medial face is concave and afforded attachment for the *flexor longus hallucis* muscle. From the distal epiphysis the bone decreases in width proximally, the change being gradual along the anterior edge but with a fairly sharp genuflexion along the posterior edge just below the dorsal limit of the specimen. From the shape of the posterior edge of the Gebel Zelten specimen it would seem that the bone was originally about as long as that of the Indian elephant. It differs from the latter, however, in that the distal extremity of the Gebel Zelten specimen is half as wide again.

Tarsal bones. MacInnes (1942) described an astragalus, two naviculars and an external cuneiform from Rusinga and attributed them to the taxon *Prodeinotherium hobleyi*. Comparison of the astragalus (M.21880) with mastodont astragali from Gebel Zelten and East Africa and with the astragalus facets of mastodont and deinotheria tibiae confirms MacInnes' identification. The external cuneiform and navicular differ both in size and in some morphological features from the equivalent bones of the Indian elephant but are likely to have belonged to *Mastodon angustidens*.

Astragalus. The deinotheria astragalus is more equant than that of *Mastodon*. The dorsal and medial surfaces bear a rectangular convex facet for articulation with the tibia. This facet is as long but less wide and more convex than that of *M. angustidens*. The anterior border of the *Prodeinotherium* astragalus from Rusinga is broken but the missing portion was probably of similar appearance to that of *Mastodon* except that the groove on the craniomedial surface, separating the tibial facet from the navicular facet, was less deep and less wide than in *Mastodon*. There are three facets on the distal surface—a triangular and convex navicular facet and two calcaneum facets. In *Prodeinotherium* the navicular facet extends to the craniomedial border of the astragalus, the medial edge of the facet being concave. The medial tip of the navicular facet of *Mastodon* is also concave but extends less

far medially. The groove separating the navicular facet from the lateral calcaneal facet is deeper but less wide than in *Mastodon*. The lateral calcaneal facet is triangular and is flatter than that of *Mastodon*. The caudomedial calcaneum facet is oval and concave. It is separated from the lateral facet by the continuation of the same groove that separates the latter from the navicular facet. The medial calcaneal facet is separated from the navicular facet only by a very shallow groove and extends posteriorly onto the under surface of the massive posteromedial projection. On the lateral surface of the astragalus the facet for articulation with the fibula appears to be as long as, but much wider than, that of *Mastodon*.

TABLE 20

Astragalus measurements

Parameter	<i>P. hobleyi</i> M.21880	<i>D. giganteum</i> (Höwenegg)	<i>M. angustidens</i> M.26658	<i>E. maximus</i> U.B. 20189
Length lateral edge	7.9	—	7.4	7.4
Length medial edge	11.0	16.0	7.8+	10.2
Maximum width	10.9+	17.7	10.0*	11.5
Depth medial edge	7.1	9.5	7.1	7.9
Depth lateral edge	4.4	7.4	3.2	4.4
Length tibial facet	6.9	—	7.3+	6.9
Width tibial facet	7.3	—	8.3	8.3

SKELETAL EVIDENCE ON THE LOCOMOTION OF DEINOTHERES The limb material of the Gebel Zelten deinotheres is too fragmentary to permit a detailed functional analysis. Nevertheless, comparison of these specimens with other *Prodeinotherium* and *Deinotherium* remains affords some information about the locomotion of these animals. The most important skeletal elements in this respect would appear to be the scapula, femur, manus and pes.

Smith and Savage (1956) determined that in graviportal mammals the scapula tends to be high and broad to afford sufficient surface area for the *serratus* and other shoulder muscles. They noted that the scapula blade of graviportal mammals is frequently expanded posteriorly to increase the mechanical advantage of the main retractor muscle of the forelimb (the *teres major*) and that the spine is usually heavy and may bear a posteriorly projecting flap in the region overlying the infrapinnous fossa (*Rhinoceros*, *Brontops*). Alternatively the spine may end in a large acromion (*Loxodonta*, *Uintatherium*). The *trapezius* muscle originates on the spine and metacromion, the *deltoid* on the acromion. Both these muscles aid in abducting the forelimb.

Compared with the scapula of *Elephas maximus*, the scapula of *Prodeinotherium hobleyi* (text-fig. 14) is less tall (51 v 62 cm) and less broad (25 v 42 cm). The caudal angle is sited more dorsally above the head of the scapula (25 v 15 cm) and is less elongate posteroventrally from the spine (26 v 30 cm). Because the caudal angle of the scapula is sited more dorsally in *Prodeinotherium* than in *Elephas*, the mechanical advantage of the *teres* muscle is thereby decreased. Smith and Savage (1956) have shown that the mechanical advantage of the *teres* muscle is equivalent to the length of the moment arm of the *teres* muscle divided by the perpendicular distance

from the glenoid to the ground. The mechanical advantage of the teres muscle of the Indian elephant is nearly $1/13$ but that of *P. hobleyi* is $1/16$.

The supraspinous fossa of *Prodeinotherium hobleyi* is relatively smaller than that of *Elephas*, and the scapular spine rises less abruptly and more dorsally. An acromion process is developed on the spine of the *P. hobleyi* scapula and is sited more dorsally than in *Elephas*. A metacromion is also present, sited level with the base of the acromion and forming a flap overhanging the infraspinous fossa. Both acromion and metacromion are reduced in comparison with those of the Indian elephant. Behind the metacromion the spine of *P. hobleyi* is broader and more robust than in the Indian elephant.

The supraspinous fossa of *D. giganteum* from Valladolid, Spain, is even more reduced than that of the Gebel Zelten deinother. The caudal angle of the *Deinotherium* scapula is less posteroventrally produced than in the extant elephants and, significantly, there are no processes diverging from the relatively slender spine. The absence of acromion and metacromion was also noted by Stefanescu (1899) on the scapula of *D. 'gigantissimum'* from Manzati, Rumania. Reduction of the spine and supraspinous fossa, and the absence of acromion and metacromion would in artiodactyls be regarded as evidence of cursorial modification (Smith & Savage, 1956).

The retention of a rigid body axis is essential in animals of elephantine bulk in order to support the weight of the body. The method of rapid locomotion is thus limited to a fast amble or trot. The more rapid action of the teres muscle of deinotheres when taken in conjunction with other features of the scapula does, however, suggest that *Deinotherium* was potentially capable of more rapid locomotion than the elephantoids. Such an interpretation is supported by other features of the appendicular skeleton and tallies with Tobey's (1962) interpretation of the function of the *Deinotherium* manus and pes. *Prodeinotherium*, although more typically graviportal than *Deinotherium*, shows some signs of cursorial adaptation.

The humerus of the Gebel Zelten *Prodeinotherium* must have been slightly shorter than that of the Indian elephant but was still appreciably longer than the ulna. The shaft of the humerus is compressed laterally and elongated anteroposteriorly in direct contrast to the condition in *Elephas*. The lateral epicondyle is shorter than in *Elephas* but projects farther laterally. The condyles of the distal epiphysis have a greater degree of curvature in *Prodeinotherium* than in *Elephas* suggesting that the ulna of *P. hobleyi* may have been capable of being flexed through a greater angle.

The ulna of the Gebel Zelten deinother is of similar length to that of the Indian elephant but is proportionately stouter. As in the elephantoids the nearly vertical alignment of the forelimb requires an olecranon process that diverges at right angles from the shaft. There is no evidence to suggest that the ulna was fused to the radius at its distal end although fusion at this point would seem likely. The distal epiphyses of both the ulna and radius were proportionately more massive in *Deinotherium* than in *Prodeinotherium*.

The radius of *Prodeinotherium* is best known from Maboko Island, Kenya, that from Gebel Zelten being represented only by the head. *Prodeinotherium* radius M.15429 is again about the size of that of *Elephas maximus*. It is less straight proximo-distally and craniocaudally than in the elephantoid proboscideans. The

radial tuberosity is less well developed than in *Mastodon angustidens* and the interosseous ridge diverges halfway down the shaft. The radius shaft of both *Mastodon angustidens* and *P. hoblelyi* is relatively wide laterally and compressed craniocaudally, but, whereas the mastodont shaft retains this shape throughout its length, that of *Prodeinotherium* becomes progressively more equant distally.

Only the large carpal bones of *Prodeinotherium* have been examined. These are serially arranged and are smaller but similar in shape to those of *D. giganteum* from Höwenegg, Germany (Tobain, 1962). The morphology of the proximal surface of the cuneiform suggests that the medial malleolus of the ulna extended farther distally in deinotheres than in elephantoids. No metacarpals have been collected from Gebel Zelten but a limited amount of information about the metacarpals may be gleaned from the distal row of carpal bones. In the unciform the facet for McV is proportionately larger and less laterally orientated than in the Höwenegg *Deinotherium* specimen and the facet for McIII is smaller. The magnum of *Prodeinotherium* bears a large facet for McIII and a smaller and more laterally aligned facet for McII.

Ehik (1930) described metacarpal fragments of *P. bavaricum* from Kotyhaza, Hungary. These were laterally compressed, but less so than the metacarpals of *Deinotherium giganteum* from Pikermi, Greece, described by Dietrich (1916). The metacarpals of *P. bavaricum* are less elongate than those of *D. giganteum* and resemble more closely those of *Elephas*. Whereas Dietrich (1916) and Tobain (1962) stated that the first metacarpal of *D. giganteum* is sufficiently reduced to suggest functional tetradactyly of the manus, Ehik alleges that in *P. bavaricum* the fifth metacarpal shows the greatest reduction. The distal articulation surface of the fourth metacarpal of *D. giganteum* is concave but that of *P. bavaricum* is concavoconvex. Ehik (1930 : 12) implies that the manus of *P. bavaricum* was more plantigrade than that of *D. giganteum*.

The metacarpals of *D. giganteum* are dolichopodous (Tobain, 1962). Whereas the proximal epiphysis of the fourth metacarpal of *D. giganteum* is orientated at right angles to the longitudinal axis of the shaft of the bone, the proximal epiphysis of McIV of *P. bavaricum* is aligned obliquely to the longitudinal axis of the shaft. The digits of *P. bavaricum* must therefore have spread farther laterally, were probably more uniform in size and are likely to have been less digitigrade than those of *D. giganteum*. The trapezium and trapezoid bones of *Prodeinotherium* have not been examined and it is therefore impossible to say if the first metacarpal was reduced as in *D. giganteum*.

The long bones of the hind limb of the deinotheres are similar in many respects to those of the elephantoids. The head of the femur is vertically aligned and, as in other graviportal mammals, the femur is longer than the tibia. Osborn (1929 : fig. 670) formulated the general rule that, relative to the length of the tibia, the femur of cursorial mammals shortens with increase in potential speed while the pes elements become more elongate. The femur and tibia of *Prodeinotherium* are of comparable lengths to those of *Elephas maximus* but the femur of *D. giganteum* from Valladolid is relatively shorter with respect to the tibial length. The tibia/femur ratio of *E. maximus* is 0.55 whereas that of *D. giganteum* is 0.71, indicating that the femur of

D. giganteum is about 30% shorter than that of the extant Indian elephant. Reduction of the first metatarsal in *Deinotherium* was noted by de Pauw (1908), and the narrow elongate pes of *D. giganteum* in conjunction with the dolichopody of the digits convinced Tobey (1962) that *D. giganteum* was capable of swifter locomotion than its contemporary elephantoids. The reduction in length of the *Deinotherium* femur would appear to support Tobey's interpretation.

The equant tibial facet of the astragalus of all deinotheres taxa from which this bone is known is a distinctive character that reflects the comparatively narrow width of the pes of deinotheres compared to that of elephantoids. The tibial facet of *Prodeinotherium* astragali is more convex than in astragali of its contemporary elephantoids but that of *Deinotherium* is flatter. The large posteromedial projection from the *Prodeinotherium* astragalus is not present in either *Mastodon* or *Elephas* and is reduced in *Deinotherium*. The surfaces of the *Prodeinotherium* astragalus that articulate with the fibula and medial malleolus of the tibia are larger and more vertically orientated than in *Mastodon angustidens*.

IV. CONCLUSIONS

The family Deinotheriidae is known from Africa, Europe and western Asia. All representatives of this family are large. Features of the skull and dentition serve to distinguish the deinotheres from the elephantoids and distinctive characters may also be seen in the postcranial skeleton. On their dental characters the deinotheres appear to be most closely related to the barytheres and moeritheres and may have been derived from ancestral *Barytherium* stock during the early Tertiary.

The family Deinotheriidae is represented by two genera, the primitive *Prodeinotherium* and the later and larger *Deinotherium*. The Gebel Zelten specimens are assigned to *Prodeinotherium hobleyi*. They include the earliest deinotheres skulls yet recovered and the fine condition of preservation of the skulls permits their use for reinterpreting the morphology of less well preserved *Deinotherium* skulls. The Gebel Zelten specimens exhibit a number of primitive deinotheres features including a steeply downturned rostrum, narrow and more anterior external nares, a skull roof that is proportionately wider and longer, less elevated occipital condyles, shorter paroccipital processes and a more vertically inclined occiput.

The facial region of *P. hobleyi* was modified for the attachment of a proboscis as was that of *Deinotherium*. The cranial region was adapted for greater movement of the skull on and with the neck than in elephantoids. The most important modifications enlarge the paroccipital processes and elevate the occipital condyles to increase the downward thrust of the mandibular tusks. Reversed curvature of the zygapophyses of the cervical vertebrae (compared to that of elephantoids) also aids in the downward movement of the head.

In detail the dental characters render the deinotheres unique. Loss of the superior pre-cheek teeth and retention of a single pair of downturned inferior tusks is a combination not exhibited by any other mammal. The main function of the tusks may have been for self defence and feeding, both involving a violent downward thrust of

the head. It would seem unlikely that the tusks were used for digging and their main function in feeding was probably for clearing and stripping vegetation. Wear facets on the anteromedial surface of the tusk tip in a number of deinotheres tusks would appear to support this interpretation. Lophodont cheek teeth have been evolved in several mammalian groups but the trilophodont anterior molars of the deinotheres are unique. The deciduous fourth premolar is also trilophodont and served as a shearing tooth in contrast to the crushing function of the second and third milk premolars. The anterior permanent molar initially serves as a shearing tooth but after the posterior molars have been erupted it becomes part of the anterior crushing battery. The second and third molars are bilophodont and persist as shearing teeth until the lophs are removed by wear. The angle of shear changes from nearly vertical in newly erupted teeth to almost horizontal in greatly worn teeth. The shearing surface is maintained by thegnosis. There is no increase in hypsodonty or brachyodonty throughout the recorded history of the deinotheres, and the length versus width parameters of the teeth of all deinotheriid taxa remain constant.

Deinotheres vertebrae are unfortunately rare but the axis and atlas vertebrae are known. They may readily be distinguished from those of the elephantoids and are modified to provide large attachment areas for the muscles of the neck. The zygapophyses of the cervical vertebrae have reversed curvature relative to those of the elephantoids. The neural spines of the anterior thoracic vertebrae were apparently longer and more posteriorly inclined than those of contemporary elephantoids. Differences from elephantoid structure may also be seen in the appendicular skeleton, the scapula and foot bones being most distinctive, the long bones less so. Advanced characters shown by *Deinotherium* include reduction of the scapular spine, elongation of the carpals, tarsals and metapodials, elevation in posture of the manus and pes and reduction of the first digit leading to the functional tetradactyly of the feet. Many of the limb modifications point to a cursorial adaptation of *Deinotherium*, but *Prodeinotherium* resembles *Elephas* in the size and proportions of the long bones.

Prodeinotherium and *Deinotherium* are separated on the basis of size, minor modifications of the dentition and characters of the skull and postcranial skeleton. Six species are recognized: *P. hobleyi*, *P. bavaricum*, *P. pentapotamiae*, *D. giganteum*, *D. indicum* and *D. bozasi*. Each species is based primarily on geographic distribution. The conservative dental characters of deinotheres are of little use for specific differentiation but the skulls and skeletal elements may prove more diagnostic when these are better known.

Deinotheres must have originated in Africa during the early Tertiary but are first known from the early Miocene. During the early Miocene *Prodeinotherium* migrated from Africa via the Middle East (and perhaps the western Mediterranean) into Eurasia. By the late Miocene *Deinotherium* had appeared. Possibly two species evolved separately, *D. giganteum* from *P. bavaricum* in Western Europe and *D. indicum* from *P. pentapotamiae* in western Asia. More probably *Deinotherium* was derived from *P. bavaricum* and then spread eastwards. *Deinotherium* and *Prodeinotherium* coexisted in Eurasia during the late Miocene. *Prodeinotherium* had become extinct in Eurasia by the end of the early Pliocene and *Deinotherium* by the middle Pliocene.

P. hobleyi was present in East and North Africa during the early Miocene but was thereafter restricted to East Africa. It survived into the Pliocene but is not known to have coexisted with *D. bozasi* which had appeared by the beginning of the Pleistocene. Whether *D. bozasi* evolved *in situ* or represented the southerly migration of the Eurasian deinotheres cannot yet be determined but the former seems more likely in view of the limited distribution of African deinotheres after the early Miocene.

Both *Prodeinotherium* and *Deinotherium* were browsing mammals that used their tusks and probosces to gather food. The proboscis of *Prodeinotherium* was smaller, and the skeleton lacked many of the cursorial adaptations of *Deinotherium*. *Prodeinotherium* probably inhabited more densely vegetated regions while *Deinotherium* frequented more open territory. There is no obvious successor to *Deinotherium* in the middle or late Pleistocene of Africa. Whether it failed to adapt to changing environmental conditions or was supplanted through competition from a group or groups of smaller herbivorous mammals must remain a matter for conjecture.

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